

THE (1692)
PRINCIPLES
OF
PLANT-TERATOLOGY

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VOLUME II

LONDON
PRINTED FOR THE RAY SOCIETY

AND SOLD BY
DULAU & CO., LTD., 37, SOHO SQUARE, W.

1916

SW

PRINTED BY ADLARD AND SON AND WEST NEWMAN,
LONDON AND DORRING.

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GLOSSARY.

- Achene*.—A dry, indehiscent, one-seeded fruit consisting of one or two carpels.
- Actinormorphic*.—Regular, symmetrical.
- Acyclic*.—Of a flower whose members are arranged spirally.
- Adelphous*.—Of an androecium whose stamens are all or in part united by their filaments.
- Alar*.—Relating to the "wing"-petals.
- Anatropous*.—Of an ovule which is completely inverted.
- Androecium*.—The stamen or stamens.
- Annulus*.—In *Stapelia* the circular outgrowth on the upper surface of the gamopetalous corolla.
- Apetalous*.—Devoid of petals.
- Apocarpous*.—Having separate, distinct carpels.
- Axial*.—Of shoot-nature.
- Axile*.—Relating to placentas situated in the central axis of the ovary.
- Basipetal*.—Towards the base.
- Bisymmetric*.—Symmetrical in two planes at right angles to each other.
- Bracteal*.—Of the nature of, or derived from, bracts.
- Bracteomania*.—The condition in which an excessive number of bracts are formed.
- Bracteose*.—Furnished with bracts.
- Caducous*.—Soon falling off.
- Calycanthemy*.—The change by which the calyx assumes the colour and consistency of the corolla.
- Campanulate*.—Bell-shaped.
- Capitulum*.—A spike in which the internodes of the axis and the stalks of the flowers have become suppressed.
- Carpelloid*.—Partially changed into a carpel.
- Catacorolla*.—A petaloid outgrowth of the inner or outer side of the gamophyllous perianth of *Narcissus*, *Gloxinia*, etc.
- Caulescent*.—Having a stalk or stem.
- Chloranthy*.—The change of all the floral members into leafy structures.

- Chorisis*.—Division, fission.
- Column*.—In Orchids, the central portion of the flower consisting of the union of the styles and stamens to form a single body.
- Connective*.—The sterile portion of an anther conjoining the loculi.
- Connivent*.—Of a whorl of members which incline towards a common centre.
- Corolla*.—The circular rim or "trumpet" inserted on the inner surface of the perianth of *Narcissus* at the mouth of the tube.
- Cortex*.—The tissue of the stem between the epidermis and vascular cylinder.
- Corymb*.—A racemose inflorescence in which all flowers are at the same level, due to the progressively greater length of the pedicels of the flowers as they become inserted at a lower level on the rachis.
- Cupule*.—A cup-like structure enclosing a fruit, and formed either by an axis or foliar organs.
- Cyclic*.—Of a flower whose members are arranged in whorls.
- Cyme*.—A definite inflorescence whose growth is terminated at every stage by a flower.
- Diadelphous*.—Of an andræcium whose stamens are united into two sets.
- Diagonal*.—Relating to floral members situated in the position intermediate between median and lateral.
- Dialypetalous*.—Having free, unjoined petals.
- Dialyphyllous*.—Having free, unjoined perianth-members.
- Dialysis*.—Solution into the original component parts.
- Dichasial*.—Of a cyme whose development at each stage is continued by the outgrowth below, and on either side of, the terminal flower of two equal axes, each ending in a flower.
- Didynamous*.—Having two long and two short stamens.
- Dithecæ*.—Of an anther which possesses the usual number of loculi.
- Drupe*.—A stone-fruit consisting of a fleshy mesocarp and a woody endocarp.
- Enneandrous*.—Having nine stamens.
- Epipetalous*.—Occurring opposite the petals.
- Epiphyllar*.—Occurring on a leaf.
- Episepalous*.—Occurring opposite the sepals.
- Etærio*.—An aggregation of drupelets resulting from the ripening of the apocarpous pistil of *Rubus*.
- Etiolated*.—Blanched, devoid of chlorophyll.

- Extrorse*.—Of an anther which dehisces towards the outer side of the flower.
- Filiform*.—Thread-like.
- FronDESCENT*.—Foliaceous, leafy.
- Funicle*.—The stalk of an ovule.
- "Gamo-gemmie."*—The "intimate association of two or several floral rudiments."
- Gamophyllous*.—Having the members of the perianth united.
- Gamosepaly*.—The condition in which the sepals are congenitally united.
- Genetic spiral*.—The hypothetical line passing through the point of insertion of foliar organs on an axis, which are spirally arranged in the order of development.
- Gynandrous*.—Having the stamens and styles united to form a column.
- Gynœceum*.—The pistil.
- Gynophore*.—The extension of the floral axis between the stamens and the pistil.
- Hemi-peloric*.—Of flowers with bisymmetric pelory.
- Heptandrous*.—Having seven stamens.
- Heteropetalody*.—The change from one kind of petal into another.
- Heterosepalody*.—The change from one kind of sepal into another.
- Hose-in-hose*.—Having the corolla enclosed by a calyx of the same colour, consistency, and development as itself.
- Hypanthium*.—The gamophyllous portion of the perianth immediately above the ovary in *Enothera*.
- Hypogynous*.—Inserted below the ovary.
- Indusium*.—The membranous covering of the sorus in Ferns.
- "Keel."*—The structure resulting from the union of the two anterior petals of the flower of Papilionaceæ.
- Labellum*.—The posterior (in the original untwisted flower) or anterior (in the usual twisted flower) modified petal or "lip" of the orchid-flower. The anterior petaloid stamen of the inner whorl of the flower of Zingiberaceæ.
- Labellum-pelory*.—The change by which an orchid-flower tends to become symmetrical owing to the transformation of the lateral petals into labella.
- Ligulate*.—Tongue-shaped, referring to the one-sidedly developed corolla of some of the florets of Compositæ.
- Loculus*.—A compartment of an anther or an ovary.
- Lodicules*.—The scale-like organs, one to three in number, occurring between the andrœcium and the paleæ in the grass-flower, which represent a reduced corolla.

- Megasporangium*.—The homologue amongst Cryptogams of the nucellus of flowering-plants.
- Megaspore*.—The homologue of the embryo-sac.
- Microsporangium*.—The homologue amongst Cryptogams of the pollen-sac of flowering-plants.
- Microspore*.—The homologue amongst Cryptogams of the pollen-grain of flowering-plants.
- Monadelphous*.—Of an androecium whose stamens are all united by their filaments.
- Mono-, di-, trimerous, etc.*—Of whorls composed of one, two, three, etc., members.
- Monothecal*.—Of an anther which possesses half the usual number of loculi.
- Negative dédoublement*.—The condition in which the primordium ontogenetically tends to divide, but in which the phylogenetic tendency is towards fusion.
- Oligomerous*.—Having few parts.
- Orthogonal*.—Relating to four floral members arranged medianly and laterally.
- Ovuliferous*.—Bearing ovules.
- Paleæ*.—The scale-leaves, usually two, enclosing the lodicules and essential organs of the grass-flower, and representing, on one view, the perianth.
- Panicle*.—A much-branched inflorescence which is indefinite as regards its main axis, but definite as regards its subsidiary axes.
- Pappus*.—The white hair- or bristle-like calyx of the florets of Compositæ.
- Pedicel*.—The stalk of a single flower in an inflorescence.
- Pelory*.—The change by which an irregular or asymmetric flower has become regular and symmetrical.
- Petaloid*.—Resembling a petal, partially changed into a petal.
- Petalomania*.—The condition in which an excessive number of petals are formed.
- Phyllomania*.—The excessive formation of foliaceous structures.
- Pinnule*.—A segment of the pinna of a compound leaf.
- Pleiandrous*.—Having an indefinite number of stamens.
- Pleiotaxy*.—Increase in the number of whorls.
- Plurisporgiate*.—Bearing many sporangia.
- Polleniferous*.—Bearing pollen.
- Pollinia*.—The masses of agglutinated pollen-grains contained in the anthers of Orchids.
- Polyadelphous*.—Of an androecium whose stamens are united by their filaments into several sets.

Polyandry.—The condition in which an indefinite number of stamens obtains.

Polymery.—The condition in which many members of a whorl are present.

Polypetalous.—Having free, distinct petals.

Polyphyly.—The increase in number of the members of a floral whorl.

Positive dédoublement.—Polyphyly.

Primordium.—The immature developmental stage of an organ.

Raceme.—An indefinite inflorescence bearing stalked flowers along the rachis, the stalks of all being about equal in length.

Rachilla.—The axis of the spikelet of Grasses.

Receptacle.—In *Thalamifloræ*, the "torus," viz. the basal portion of the flower upon which all its members are inserted. In *Rosaceæ*, the "calyx-tube," viz. that part of the flower enclosing the ovary, above which the sepals, petals, and stamens are inserted.

Rostellum.—The beak-like projection from the upper part of the column in Orchids, representing the abortive anterior stigma.

Scorpioid.—Relating to a definite or cymose inflorescence in which the terminal flower occurs alternately right and left, while the axis of the whole is circinnately coiled.

Scutellum.—The intraseminal absorptive organ of the Grass-embryo, having the morphological nature of the lamina of the cotyledon.

Septate.—Of an ovary which is divided by partitions into loculi.

Serial.—Of members of a whorl disposed side by side in the median plane.

Solution.—Separation, breaking away.

Spicate.—Relating to a spike.

Spike.—An indefinite inflorescence whose flowers are sessile on the rachis.

"*Spike*" (of Grasses).—A compound spike, or sometimes a raceme.

"*Spike*" (of *Ophioglossaceæ*).—The fertile segment of the sporophyll.

"*Spikelet*."—In Grasses, the subsidiary division of the inflorescence consisting of a short rachis bearing a few flowers and enclosed by one or two glumes.

Sporangiody.—The change into a sporangium.

Sporangiophore.—The stalk, an outgrowth of the sporophyll, which bears the sporangia.

Spur-pelory.—The change by which a flower becomes symmetrical owing to all the sepals or petals becoming spurred.

Staminal.—Of the nature of, or derived from, stamens.

Staminate.—Of the nature of a stamen.

Staminode.—An imperfectly-developed or rudimentary stamen.

Staminoid.—Partially changed into a stamen.

"Standard".—The large posterior petal of the flower of Papilionaceæ.

Sympetaly.—The union of petals.

Synandry.—The union of stamens.

Synangium.—A compound or plurilocular sporangium.

Synanthy.—The union of flowers.

Synsepaly.—The union of sepals.

Umbel.—An inflorescence whose flowers are all inserted at the same level at the top of the peduncle.

Uni-, bifoliate.—Of a compound leaf with one or two leaflets.

Utricle.—In *Carex*, the bladder-like bract which completely encloses the fruit.

Venation.—Veining.

Versatile.—Of an anther which is attached to the filament by the middle of its dorsal side, and turns freely thereon.

Verticillaster.—The false whorl caused by the approximation of the two congested axillary cymose inflorescences on opposite sides of the stem of Labiatæ.

Vexillar.—Relating to the "standard" petal.

Vivipary.—The transformation of the flower into leafy buds which drop off and become independent plants.

"Wings".—The lateral petals of the flower of Papilionaceæ.

Zygomorphic.—Irregular, asymmetrical.

PRINCIPLES OF PLANT-TERATOLOGY.

IV. THE FLOWER.

As was pointed out in the first volume, we may regard the factors of simplification and reduction as having played a large rôle in the process of evolution of plant structures. The "flower," using this term in its broadest sense to include all specially modified portions of the axis on which sporophylls and accessory organs are aggregated for purposes of reproduction, it is best to regard as the final stage in the modification of a leafy shoot. We may imagine that the axis of the shoot became greatly shortened by reduction in length or obliteration of the internodes, while the leaves, many of which were probably at once green assimilating organs and sporophylls, became greatly reduced in size and complexity of organization, and modified in texture and colour. A leafy fern-shoot may have become a cone, which probably in its turn became still further modified into a typical "flower," in the more restricted sense of the term. Although it is more than probable that the Angiospermous flower was derived in the past from a cone-like structure, we know absolutely nothing as to the nature of the plants which bore such a cone.

The consideration of abnormal structures will include not only the "flower" of the Angiosperms, but also the

"cones" of Gymnosperms and Vascular Cryptogams, and the sporophylls of Ferns, which are not contained in what we usually term a "flower."

I. DIFFERENTIATION.

The simplification, referred to above, which has occurred during the process of the evolution of the flower, will tend to be counteracted from time to time by abnormal breaks in the direct line of progress, taking the form of less simple and more highly differentiated structures, some of which may, with a fair amount of certainty, be attributed to reversionary tendencies on their part—harkings-back, under the influence of this or that stimulus (the nature of which may, or may not, be discoverable), to conditions of greater complexity obtaining in the ancestry of the plants affected.

1. PROLIFERATION.

This phenomenon consists in an extension of the axis beyond its normal limits. It may assume various forms according to its degree of development or the nature of the appendages which it bears. There may be either an unbranched median extension of the axis; or there may be axillary branching without any abnormal extension of the main axis; or both phenomena may be combined.

A discussion of the subject will be entered upon after instances of the various types have been cited.

MEDIAN PROLIFERATION.

1. THE INFLORESCENCE.—This may be either reproductive or vegetative in character.

As an instance of the former may be cited the case mentioned in the 'Gardeners' Chronicle' of 1881 of a female cone of the Norfolk Island pine (*Araucaria excelsa*) the axis of which extended upwards and

developed a second cone above the first; in correlation with the production of the extra cone all the scales of the lower one were sterile.

A case in *Cryptomeria japonica* was seen in which a proliferation from a female cone bore, a short distance above it, male flowers.

In the common primrose (*Primula vulgaris*) the axis of the inflorescence is completely suppressed normally, the individual flowers arising in the axils of the rosette-leaves. But in the variety *caulescens* this axis becomes developed, bearing the flowers either in a terminal umbel* or more or less scattered along it.

In those species, *e. g.* the cowslip (*P. veris*) and *P. obconica*, whose inflorescence normally consists of a simple umbel, proliferation may occur whereby one or more supernumerary umbels may be formed (Pl. XXVI, figs. 1 and 2). In other species, *e. g.* *P. japonica*, this structure is the normal one.†

In proliferated spikes of the plantain (*Plantago*) the main axis often becomes elongated much beyond its normal height.

Central or median proliferation of the flower-heads or capitula of the Compositæ and other orders has from time to time been seen. In view of the fact that these heads represent extremely congested and shortened spicate inflorescences it is not surprising if occasionally the restraint of this extreme condition is, as it were, swept aside, the axis extending its normally suppressed internodes in order to form a fairly elongated structure. This has been observed in the daisy (*Bellis perennis*), in which a second capitulum was formed above the first; and in *Echinacea serotina* central proliferation of the secondary capitula occurring in the axils of the involucre bracts has been observed. But in these cases the capitula themselves do not appear to have been changed in their constitution. Abnormal formation of

* The "polyanthus" condition.

† A good example of the widely-occurring phenomenon, first called attention to by St. Hilaire, that what is abnormal in one species or genus may often be the normal feature in an allied one.

the internodes in the head itself would appear to be a rare phenomenon. Weber has observed the flower-head of the Dutch clover (*Trifolium repens*) transformed by this means into a loose spike. Kirschleger saw the same thing in the field-eryngo (*Eryngium campestre*). The cause of the infrequency of solution of the capitulum into a loose spicate inflorescence may be that axillary proliferation of these capitula is so frequent.

Henslow describes and figures a very good example of a spike of the mignonette (*Reseda odorata*) becoming, by proliferation of the flowers into racemes or panicles, and elongation of the main axis of the spike, transformed into a complex paniculate inflorescence. Much the same sort of thing he describes in the dark mullein (*Verbascum nigrum*).

In the rye-grass (*Lolium perenne*) the "spikelets," representing congested inflorescences, may each proliferate into a "spike" whose "spikelets" in their turn may do the same; in this way arise the varieties *compositum*, *ramosissimum*, and *paniculatum*.

Schmitz made some most interesting observations on abnormal inflorescences of the cypress-spurge (*Euphorbia Cyparissias*) which confirmed the conclusions reached by Warming as a result of researches on the development. It is now recognized that the "cyathium" of *Euphorbia* is an inflorescence, consisting of a highly congested axis, bearing externally an apparent whorl of small involucre bracts alternating with large glands. Within are several scorpioid cymes of male flowers surrounding a central female flower. Schmitz observed instances in which the internodes between the involucre bracts (normally suppressed, and thus causing them to become verticillately arranged) had become developed, the bracts being spirally arranged at wide vertical distances apart on the axis, and each bearing in its axil a stamen (Pl. XXIX, fig. 1). This last fact proves that the supposed stamen of *Euphorbia* is in reality an entire flower. As there is no articulation present in these axillary "stamens," the

stamens proper consist of sessile anthers at the apex of the whole.

In other cases this author found that the axillary product of the bract in this position was, not a stamen, but an inflorescence, the main axis of which terminated in a cyathium; in the axil of a leaf borne by this axis was a "stamen"; this "stamen" in its turn bore two leaves, in the axil of the lower of which was a second "stamen" bearing a leaf. This whole structure, representing a proliferated male flower, is of the greatest interest and importance, for it may be regarded as a reproduction of the structure (or part of it) of the original cyme of male flowers from which each of the five cymes of male flowers in the normal cyathium has been derived by means of excessive reduction, consisting of complete suppression of the internodes and elimination of the bracts.* In *Anthostema* the normal inflorescence is less congested than in *Euphorbia*, and the bracts of the scorpioid cymes are present and well developed.

In the common larch there was observed a long-drawn-out female cone due to the great development of the internodes between the scales. The structure was barely recognizable as a cone; it was caused by an excessive flow of nourishment induced by the presence of the insect *Thrips laricis*.

Vegetative proliferation of the inflorescence is very common. For example, in the larch it may assume considerable dimensions, bearing numbers of ordinary needles above the cone proper, in which case the cone itself is correspondingly reduced and abortive (Pl. XXVII, fig. 1).

The phenomenon is extremely common in the female cones of *Cryptomeria japonica*.

In *Cephalotaxus* the biovulate "flowers" are grouped in an inflorescence in the axils of scale-leaves. This primary axis of the inflorescence sometimes proliferates, bearing foliage-leaves and a terminal bud.

* These are still sometimes present in the form of small scales.

In some of the plantains (*Plantago major* and *P. lanceolata*) the apex of the spike may develop further to form a rosette of foliage-leaves. A similar phenomenon is seen in the lupin (Pl. XXVI, fig. 3).

Good instances of *normal* vegetative proliferation are the pine-apple (*Bromelia Ananas*) and the bottle-brush (*Callistemon*).

2. THE FLOWER.—Here also the proliferation may be reproductive or vegetative.

In the case of the former, in many plants the floral

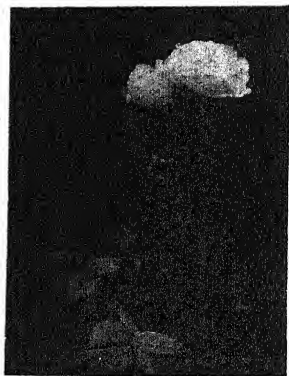


FIG. 61.—*Rosa centifolia* (Garden Rose). Proliferation of flower into a small inflorescence bearing two roses.

axis may elongate and produce an entire inflorescence, as in *Trifolium repens* and in many Compositæ, *e.g.* the "hen-and-chickens"-daisy (*Bellis perennis* var.), and the sneeze-weed (*Helenium autumnale*). In the plantains, most pronounced in *P. major*, the individual flowers of the spike develop into branches whose flowers may do the same until sometimes as many as six or seven generations of branches may constitute a complex panicle replacing the normal spike (Pl. XXVII, figs. 2 and 3).

In the feather-hyacinth (*Muscari comosum*) there is a remarkable variety in which the flowers of the spike are replaced by delicate, elongated branches which are

themselves again branched in the same way; the branches, representing pedicels, are filamentous, and both these and the numerous bracts are purplish in colour, and formed at the expense of flowers, which are entirely absent. This, therefore, is a structure intermediate between a reproductive and a vegetative proliferation. Fig. 61 shows a rose-flower proliferated to form an inflorescence of two flowers.

In the sedge (*Carex glauca*) the exceedingly reduced axis of the "utricle" has been described as produced into a "spike," either male, female, or androgynous.

Schmitz observed, in the abnormal *Euphorbia* previously referred to, some of the axillary "stamens" proliferating into complex inflorescences.

We come next to the phenomenon of proliferation into a flower.

It is not uncommon for the cone of *Equisetum* to form a second cone above the first.

The uni- or biovulate axis of the maidenhair tree (*Ginkgo biloba*) may proliferate in the sense that it bears a greater number of ovules which then become stalked and may be spirally arranged.

In *Cephalotaxus*, flowers on a tree in Windsor Park were observed which, instead of forming merely the two normal ovules, one on each side of the rudimentary apex, had proliferated slightly so as to form a third ovule at a higher level; or, the two normal ovules being replaced by tiny leaves, a second pair of ovules decussating with these had developed above.

A precisely similar flower may be formed at a varying distance above the first, as in the rose (Pl. XXVIII, fig. 4), *Ranunculus*, and *Trollius*. Or, this phenomenon may be extended and the proliferation repeated over and over again, so that a number of flowers may be formed one above the other, as in a wallflower in which every flower, which was unusually small and provided with calyx and corolla only, had proliferated from five to seven times, as indicated by the articula-

tions left on the axis (fig. 62). It is a common occurrence in the "double" form of *Arabis albida*.

A less pronounced type of proliferation is that in which the floral axis is, not necessarily less extended, but less independent and differentiated after growing beyond the confines of the normal flower. In the above-cited cases we see a new flower-bearing axis arising out of the first; but in those about to be mentioned the extended axis is part of the normal

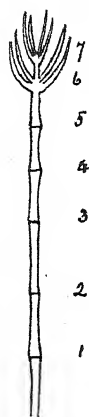


FIG. 62.—*Cheiranthus Cheiri* (Wallflower). Continuous proliferation of floral axis to form a concatenation of seven flowers. (Diagrammatic.)

flower. In a columbine (*Aquilegia*) the floral axis was considerably elongated, forming a naked length, beyond which it bore several carpels of modified form and coloration. In the Kew Herbarium some specimens of *Brassica campestris*, collected by Aitchison in Kashmere, were seen in which the flowers, otherwise normal, had developed a gynophore which was often as much as two inches long. This is a particularly interesting phenomenon in view of the fact that in the closely allied order Capparidaceæ this structure is a perfectly normal feature.* But this abnormality becomes less astonish-

ing when we find that in *Diplotaxis Harra*, a member of the Cruciferae, a long gynophore is present as a normal feature.

But a combination of the two conditions may frequently occur. Some flowers of water-avens (*Geum rivale*) nearly all proliferated to form a second flower; in one flower all the carpels had become transformed into small purplish lanceolate leaves spirally arranged in great numbers to form the calyx† and involucre

* St. Hilaire's law again.

† The utilization of the ovary of the primary flower for the calyx of the

of the second flower above: the lowest of these leaves still retained a rudimentary stigma. In other flowers the petals had become separated and spirally arranged on the proliferated axis. It is an interesting fact that a gynophore is normally present in this species; hence there probably resides in its flower a greater natural tendency to proliferate than in that of the other species.

Velenovsky raises an important issue in connection with this abnormality of *Geum*. The receptacle remains unaltered; the proliferated axis is of the same character as the axis below the flower, and is obviously a continuation of that axis. He points out the utter improbability of the receptacle representing a cupule (axial structure) intercalated between the two floral axes; it must therefore be of purely calycine nature, and this must apply to all Rosaceæ.

In several inflorescences of the wild mignonette (*Reseda lutea*), received by Mr. Sprague of the Kew Herbarium from near Southampton, every flower without exception had a long-stalked ovary (a feature reminiscent of the allied order Capparidaceæ) within which at the base, representing a continuation of the main axis of the flower, was a small secondary flower. In some of the abnormal flowers of *Primula sinensis* described by Masters, the calyx-tube, ovary, and free central placenta became abnormally extended; the last-named structure contained, therefore, a central proliferating axis of the flower.

The flower of the pear is, under certain conditions, peculiarly liable to proliferate; as a rule, this abnormality has been noticed only in the mature state of the flower, *i. e.* when the fruit has become well advanced in development. Owing to this fact, an adequate and complete interpretation of the phenomenon is rendered difficult if not impossible, while the observation of all the earlier stages would have made a solution of the problem easy. H. Hoffmann, however,

secondary one, and the ovary of this in its turn for the calyx of the tertiary flower, has been observed in the carnation.

has described flowers in which a second calyx was formed immediately within the first, after which succeeded the normal petals and stamens. Later stages are not mentioned by him.

The phenomenon as known in the mature condition takes the form of a series of "pears" (usually 2-4) arranged one above the other. The lowermost fruit

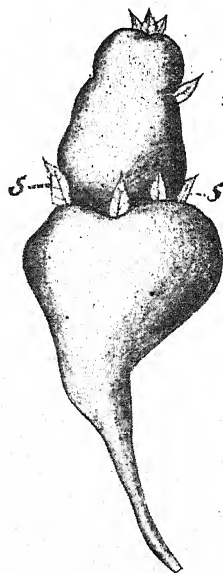


FIG. 63.—*Pyrus communis* (Pear). Proliferation to form a second pear, one of whose sepals is adnate with the ovary only part way up. (After Turpin.) s, sepals.

bears the usual five sepals (occasionally foliaceous) arranged in a wide circle at the top; the succeeding fruit or fruits may either resemble the first one or each may be subdivided into a number of partially individualized portions entirely resembling the normal fruit in consistence and colour, and each bearing at its tip a withered remnant of a foliar organ (Pl. XXVIII, figs. 1-3, and fig. 63 in text). It is usual to find an ovary (generally more or less abortive) near the apex of the uppermost fruit, but it is entirely absent in the

others; sometimes it is absent altogether. In many cases, especially where an ovary is present, the "eye" at the apex of the whole series resembles that in a normal fruit, and bears sepals.

All such abnormal pears described in the literature probably constitute essentially the same phenomenon, though an attempt has been made, by Penzig and others, to divide them into two sets, namely, those which result from the formation of distinct flowers one above the other, and those resulting from proliferation of the axis between the organs of one and the same flower. Wittmack, for instance, describes a three-storeyed pear of which he states that the lowest storey represents the calyx-, the middle one the corolla-, and the uppermost the stamen-region, the floral axis being elongated between each set of floral members; but he adduces no evidence in favour of his view. Buchenau describes a two-storeyed pear in which, according to his view, the lower bore the usual five sepals, and the upper one sixteen sepals spirally arranged on the surface of the fruit, within them at the apex being, as in the normal case, the remains of the petals and stamens, while an ovary was present inside. In an early number of the 'Gardeners' Chronicle' the spirally-arranged fleshy portions of the second storey of an abnormal pear are, by the editor, in one place described as sepals, and in another as petals and stamens. The fact is that in such an advanced stage of development it is impossible to determine with certainty the nature of the organs of the upper fruits; in some cases it may be that they represent petals and stamens. In some cases observed by the present writer there were distinct remains of petals immediately within the calyx of the lowest fruit and surrounding the base of the second one; hence this latter could not have been constituted of the petals of the lower one. The most obvious and natural solution of the phenomenon is to regard in all cases each fruit formed beyond the normal one as a distinct and sessile

flower, more or less perfect in its development. Inasmuch as the upper fruits entirely resemble in their consistence and every other essential character the normal one, it seems best to regard them as being constituted in exactly the same way. The normal pome-fruit may be regarded as composed of a central "core" (the ovary) surrounded by, and congenitally fused with, the abnormally elongated bases of the sepals. Cela-kovsky objected to the idea that the sepals played any part in the formation of the fruit of the Rosaceæ on the ground that these sepals are perfectly organized, which they would not have been had any portion of them been fused with the axis below; but he forgot that this case may be quite analogous to that of the Solanaceæ in which the leafy bract, although it is fused for a long distance with the main axis, is yet as well and fully developed as any other leaf on the plant. In both cases, besides fusion, congenital elongation of the leaf-base may have occurred. Strong support is lent to this view by an observation of Domin's in *Potentilla aurea*, in which the receptacle became split up into a number of free sepals, the base of each being furnished with stipules provided by the leaves of the epicalyx, a fact which further shows the true nature of this last-named structure. The stamens and petals were seated on the true receptacle or torus of the flower. If the sepal-bases, as proved by this abnormality, constitute the receptacular tube in *Potentilla*, it is only natural to suppose that this structure is of the same nature in all other members of the Rosaceæ.

Those kinds of pear-shoots, of which an extreme case is described and figured in the 'Gardeners' Chronicle,'* where the vegetative axis appears to assume the consistence, to a certain extent at least, of the "fruit," thus seeming to strongly support the shoot-theory of the pome, may probably be explained as follows: the shoot had, as it were, intended to form a fruit, but, owing to certain conditions

* 1881, part 1, p. 41.

which were adverse for that function, proceeded to form vegetative buds instead; a certain amount of flower- and fruit-forming substance had, however, accumulated, and became stored up in the axis below the buds.

In many abnormal pears the sepals of the would-be flower may show four distinct changes: increase in number, displacement downwards (on the proliferating axis within the "pear"), phyllody, and dialysis of the basal fleshy calyx-tube. The example figured in the 'Gardeners' Chronicle' probably represents merely a very extreme form of proliferation of the "fruit" in which the sepals have become greatly displaced, both vertically and horizontally, exposing the central proliferating axis, and in which most have become foliaceous, some bearing vegetative shoots in their axils. This will quite well explain the bizarre structure.

That the sepals take part in the construction of the normal pome-fruit seems indicated by the following facts: that the middle and peripheral tissues of the fruit are differently constituted; that the vascular bundles of the central portion and those of the calyx form separate strands below, while those intended for the petals branch off higher up from the calyx-strands; that certain varieties of apple exhibit five distinct ribs on the fruit; and lastly, that the quite similar pears of the upper storeys are often split up into separate fleshy portions, each clearly representing the basal continuation of the withered foliar organ above, which is particularly well shown by an abnormality figured in the 'Gardeners' Chronicle.' There was a case seen in which the pear was represented solely by two or three tiny swollen bases of calyx-petioles, the central axis being quite undeveloped.

There was sent to Kew a seedless apple from Colorado exhibiting an abnormal structure which goes a long way to prove the truth of the theory that the pome-fruit is in reality a calyx-tube. Alternating with the sepals at the top of this apple were five tiny partial

apples, each bearing at its tip a sepal. Each obviously represented merely the swollen fleshy base of the extra sepal, and is comparable to the fleshy portions of the disjoined pears above-mentioned. They resembled in colour and consistence the mother-apple itself. They could not possibly be of axial nature, seeing that each was prolonged above into a sepal. If they represent, as they clearly do, the sepal-bases, this must also be the interpretation of the pome itself. Doubtless the sepals in this case are transformed petals; and their presence is probably correlated with the seedless character of the fruit.

The view above set forth as to the morphology of the pome is supported by H. Hoffmann's observation in certain flowers of the pear where a second calyx was formed immediately within the first, followed by petals and stamens; this may be regarded as a second sessile flower.

The following explanation may, therefore, be applied to all abnormal pears of the storeyed type hitherto described by botanists. The axis of the flower has proliferated, thereby (as in all such cases) causing the "inferior ovary" to disappear; a second sessile flower is immediately formed within the calyx or the corolla of the first, the stamens and petals of the latter, perhaps owing to lack of adequate material, not being formed at all; in the second or subsequent flowers so formed by proliferation the calyx is constituted as in the first flower, but an ovary may or may not be present; it frequently happens, however, as a natural result, doubtless, of the abnormally-elongating axis of the extra flowers, that the fleshy sepal-bases become more or less dissociated and individualized and the entire sepals themselves displaced out of the whorled into a scattered spiral arrangement on the central axis. We occasionally see this displacement, or irregular grouping, in a normal pear where a foliar organ (best regarded as a sepal) occurs on the side of the fruit instead of in the "eye" at the apex; this fact cannot therefore, on this view,

be used in support of their position by the adherents of the theory that the pome consists solely of axial tissue.* In cases of this sort, both in the pear and cucumber, the number of sepals may be more than five: this number occurring at the top and one or more at a lower level.

In many ovaries with axile placentation it is probable that the central part of the placenta is of axial nature, representing an extension upwards, between the united margins of the carpels, of the floral axis. That such an extension may take place is proved, in certain plants, by some abnormalities. For example, in the seedless navel orange the axis is extended through the centre of the fruit and forms a second complete (as regards external conformation) but tiny orange at the top; as a rule this only partially projects beyond the rind of the parent, and is sometimes split up, or partially so, into its component carpels, just as we have seen that the pear-fruit may become partially split up into its constituent sepal-bases under similar circumstances. This second orange bears, of course, no seeds. In another orange of a different variety a small complete fruit was observed entirely enclosed within the parent; it had a perfect rind. Immediately below the small orange and closely appressed to it were some structures having the appearance of a second whorl of separate carpels.

The most elementary type of proliferation of the flower is afforded by those cases where the normally cyclic flower becomes in greater or less degree acyclic, the axis becoming abnormally elongated, and sometimes spirally twisted; good instances of this are the wheat-

* The fact that this lateral sepal frequently produces an axillary bud (which in its turn may produce a second pear) does not necessarily imply that a cupular axis is present, for with Celakovsky it is best to maintain that all axillary shoots are really adventitious on leaf-bases, and appear to be readily formed where leaf-structures make an angle with the organ to which they are attached, as in the case of leaf-segments of the tomato. On these lines can also be explained the abnormal cucumber-fruits described and figured by Masters which showed lateral proliferation; for here the lateral flowers probably arose in the axils of similarly displaced sepals, the fruit being of the same morphological nature as that of a pear.

ear carnation, and a similar form is the lily which is referred to in a later section. Less pronounced examples of axis-elongation and acyclism are afforded by the phenomenon of "spiralism" observed by

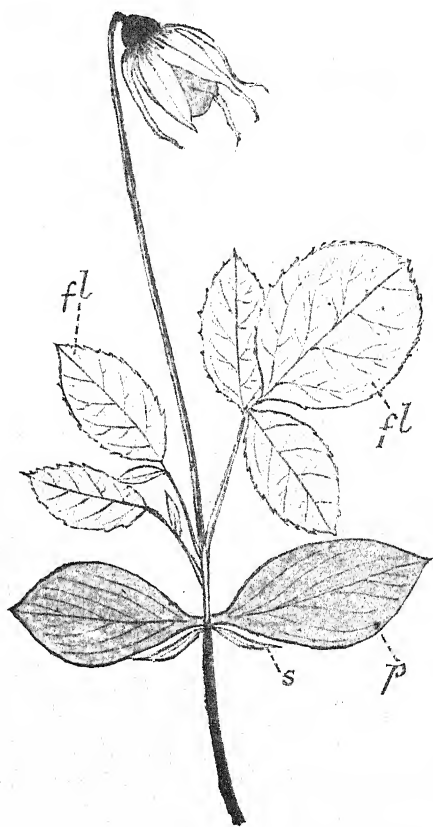


FIG. 64.—*Rosa centifolia* (Garden Rose). Proliferation of flower in which a foliage-shoot and flower have developed in place of the andrœcium and pistil. *fl*, foliage-leaves; *p*, petal; *s*, sepal.

Costerus and Smith in *Gloriosa Plantii* and by Ducamp in the American aloe (*Agave americana*).

Vegetative proliferation of the flower is quite frequent, the rose affording well-known examples; a specimen depicted (fig. 64) had a leafy shoot de-

veloped beyond the flower, of very considerable length and bearing simple leaves, each of the same size as the leaflets of a normal leaf. Pl. XXX, fig. 1, also shows a similar case in which the shoot terminates in a flower. Mr. T. A. Dymes supplied a plant of *Trifolium repens* which bore a virescent head in which each flower was transformed into a long-stalked vegetative shoot bearing two or three often imperfect leaves (composed of one or two leaflets only).

Some "flowers" of *Cephalotaxus*, each of which usually forms two ovules only, had, instead of forming these, developed into a leafy bud.

In the carnation, as a result often of hybridization, the flowers of the inflorescence all proliferate into spike-like, green, bracteose branches; this is the form known as the "wheat ear" carnation; the same thing occurs in some of the other species of *Dianthus* (Pl. XXIX, figs. 2 and 3), and also in the garden-pea.

In the pear the vegetative impulse, which produces the proliferations already described, may proceed still further, and the fruit or fruits may terminate in a leafy, vegetative shoot (Pl. XXIX, fig. 4).

In *Scabiosa atropurpurea* the terminal floret (Pl. XXX, figs. 2 and 3) of the capitulum was seen proliferating. In the specimens of *Selaginella grandis*, already in part described, many of the cones had proliferated into leafy shoots; these cones had been growing against the moist sides of the Wardian case. Goebel describes a similar instance.

Ridley observed a very interesting case in *Equisetum maximum*, where the cone had proliferated into a vegetative shoot, a phenomenon which had been observed by other botanists before him.

AXILLARY PROLIFERATION.

This may be either reproductive or vegetative. Instances of the former will first be cited, beginning with those in the axils of bracts. Chiffot cites a cone

of *Equisetum maximum* whose apex had been injured by frost, as a result of which several lateral cones were produced, giving the whole a very striking appearance.

Velenovsky describes a short-shoot as occurring in the axil of a "bract" of a larch-cone, and replacing the ovuliferous scale; this shoot bore a number of spirally-arranged fleshy ovuliferous scales.

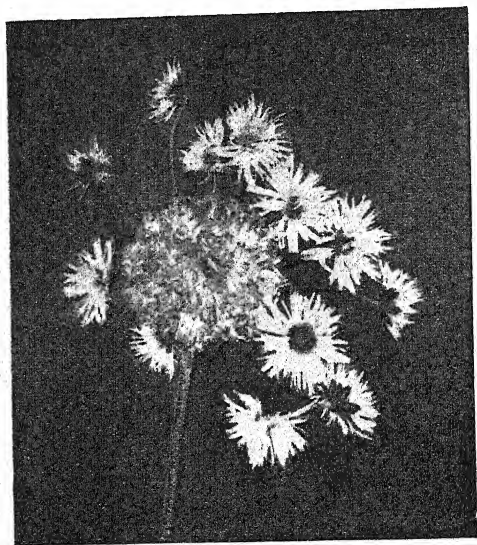


FIG. 65.—*Bellis perennis* (Double Daisy). Long-stalked secondary capitula in axils of involucre bracts. (G. Massee photo.)

Fermond mentions the occurrence in *Taxodium distichum* of a secondary female cone in the axil of a scale of the primary one.

In the maize-cob lateral secondary cobs may arise in the axils of the basal bracts or even somewhat higher, giving rise to the variety *polystachya*.

Many-flowered tulips are due to extra flowers arising in the axils of the bracts or bracteoles on the peduncle.

In the daisy (*Bellis perennis*) secondary heads were

seen arising in the axils of the involucre bracts of the normal one ("hen-and-chickens"-daisy). This is not a very uncommon abnormality in Compositæ (fig. 65). It is a normal feature in *Cladanthus*.

Graebener describes the development of flowers and shoots in the axils of the rudimentary leaves which occur on the cupular axis surrounding and enclosing the fruit in the cactus (*Opuntia Bergeriana*). In *O. Salmiana* it is extremely frequent for vegetative shoots to arise in this position. Various authors describe the formation of secondary fruits from the primary one.

From the axils of the members of the various floral whorls branches may arise which may then be either reproductive (forming a flower or an inflorescence) or purely vegetative. Those which are axillary to *sepals* will next be described.

Hua first described flowers of *Cyclamen persicum* which bore secondary flowers between the calyx and the corolla, namely, in the gaps between the sepals, this probably owing to space-requirements which did not permit of a position actually axillary to the sepals. These secondary flowers were incomplete, consisting only of two whorls: a (usually) petaloid perianth, with members reduced in number from the normal, and a whorl of stamens usually alternating with the perianth-lobes. Frequently the stamen had a small petaloid outgrowth from its exterior side; owing to this fact, to the fact, also, that these structures alternated with the perianth-members, which were sometimes green in colour, and also to the further fact that he sometimes found tertiary flowers in exactly the same position in the secondary flowers as these occupied in the primary flower, he concluded that the perianth in the secondary flowers is really a calyx. The present writer has observed the same phenomenon on two occasions (fig. 66); and, in respect of some flowers, can confirm Hua's conclusions, inasmuch as transitions were found between green sepals and petaloid structures in the secondary flowers. In the case

of other flowers, however, there was clear evidence that the petaloid leaves were petals, as the stamens were exactly opposite to them, and there were one or two extremely rudimentary structures, external to these, which could be interpreted as sepals. These flowers also differed from those examined by Hua in possessing a well-developed ovary. It is not unlikely that in some cases the sepals only, and in others the petals only, would develop. In any event, the abnormality is a rare one, especially the extra-axillary* position of the secondary flowers.

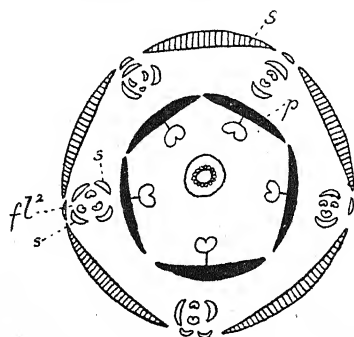


FIG. 66.—*Cyclamen persicum* (Sow-bread). Diagram of flower producing secondary flowers between the calyx and corolla. s, sepals; fl², secondary flower.

In Cruciferae it is not uncommon for flowers to arise in the axils of the sepals. Masters points out that sepals have a greater tendency than other floral leaves to produce axillary buds, which is probably due to their more foliaceous character.

Masters, in the case already cited, describes and figures the occurrence of secondary flowers in the axils of both the displaced and the normally-situated sepals of the cucumber, and from one of the sepal-axils of each such flower a tertiary flower also arose; the sepals were always foliaceous (Pl. XXXI, fig. 1).

* This is a true case of extra-axillary branching, whereas those usually cited in text-books are not so.

Proliferation in the axils of *petals* is illustrated by the following cases.

A pink (*Dianthus plumarius*) has been seen with flowers in this position. Masters figures a flower of *Dianthus* sp. with small inflorescences occurring in a similar position; they were formed at the expense of the andrœcium which was completely suppressed. In double flowers of *Spiræa prunifolia* rudimentary flowers occur in the axils of the petals.

Masters describes a cucumber in the male flowers of which long shoots occurred axillary to the petals which produced stalked secondary flowers.

Turpin figures a flower of *Celastrus* in which every petal has a flower in its axil (Pl. XXIX, fig. 5).

Proliferations axillary to *stamens* are seen in the following.

Masters figures a long-stalked flower arising from the axil of an ordinary stamen in *Nymphæa Lotus*. In *Begonia Pearcei* inflorescences were observed in the axils of several of the stamens of a flower; in this case the phenomenon is less surprising inasmuch as the stamens were semi-foliaceous.

As an instance of flowers produced in the axils of *carpels* there may be mentioned the case of a wild mignonette (*Reseda lutea*) of which Celakovsky gives an interesting figure.

Axillary vegetative proliferation will now be considered, and firstly, in relation to *bracts*.

Abnormal axillary branching is very frequent in the Coniferæ. Parlatores illustrates a case in *Pinus Lemoniana* in which, in place of the ovuliferous scales, 2-needed short-shoots were situated in the axils of the "bracts." This seems to represent the extreme vegetative condition of an axillary production of rudimentary shoots, which has given rise to a wide discussion as to the nature and origin of the ovuliferous scale in certain groups of the Coniferæ and has led to an interpretation thereof which hitherto has had the greatest number of adherents.

The phenomenon, as described, for instance, by Stenzel and Willkomm, consists in the appearance of an extremely short shoot in the axil of the bract, bearing, apparently, the two halves of the ovuliferous scale as its two first transversely-placed leaves; this is the main feature of the phenomenon and further detail need not be gone into. These two lowest appendages of the axillary shoot clearly represent the ovuliferous scale which is cleft asunder, the two halves being carried out of their normal median position into a transverse one owing to the appearance between them of the axillary bud; in other examples the bud raises them up some way above the level of the "bract," and they may become more or less leaf-like, the ovules at the same time becoming either completely suppressed or imperfectly developed (Pl. XXXI, figs. 2-6). These appendages may even become united together on the adaxial side of the shoot. This abnormality has been observed chiefly in *Larix europæa*, *Tsuga Brunoniana*, *Picea excelsa*, and *Pinus* sp.

Alexander Braun, in 1842, was the first to utilize this phenomenon for the interpretation of the ovuliferous scale and the female "cone" generally. He held that the latter is essentially an inflorescence and not a simple flower as in the case of the male "cone;" and that the ovuliferous scale represents the two first transversely-placed leaves, which were carpels, of an axillary shoot which, on complete suppression of the carpels, became fused by their posterior (*i. e.* adaxial) margins,* the double carpel thus resulting inevitably becoming adpressed to and basally united with the corresponding, *i. e.* ventral or upper, surface of the "bract." Elaborate observations and interpretations on the same main lines were subsequently made by Caspary, Stenzel, van Tieghem (in part), Willkomm, Engelmann, Parlato, Velenovsky, and Celakovsky. The last-named author especially, by a most

* Cf. precisely the same phenomenon observed by Klein on foliage-shoots of *Calycanthus* and *Calendula* as described in vol. i of this work.

comprehensive and ingenious treatment of the whole subject, created what may be regarded as an impregnable position for the view originally enunciated by Alex. Braun. By a careful study of the series of abnormalities he has displayed a continuous and gradual transition (and this is the important point) between the first two leaves of the axillary shoot and the normal ovuliferous scale. He has also clearly shown that in *Pinus* a third anterior leaf of the axillary shoot, revolving through 180° , takes part, along with the first pair of leaves, in the formation of the ovuliferous scale.* Velenovsky observed in proliferated larch-cones an axillary shoot which bore not only the two fleshy transverse ovuliferous leaves, but also a number of other similar leaves, each bearing an ovule on its lower surface. This fact certainly supports Braun's theory.†

Celakovsky regards the ovuliferous scale in the Araucarieæ, where it is clearly not a compound but a single organ, bearing but one ovule, as consisting of a single leaf of the first leaf-pair of the axillary bud. This will explain the presence of the unique ovule. The same explanation is probably applicable to the case of the Podocarpeæ where but a single ovule also occurs.

In the Taxodineæ the scale often consists of several parts, representing the fusion of more than three leaves of the axillary bud. In the Cupressineæ the interpretation is the same as for the Abietineæ.

In the Araucarieæ and some Taxodineæ, *e.g.* *Sequoia*, there is every appearance of there being but a single scale present and not two fused together. And in the former group there are no abnormalities known which might indicate what the true state is. Celakovsky reaches his conclusion on comparative grounds. Velenovsky, while agreeing with him,

* With this should be compared the curious axillary scales of an abnormal pine-cone described in vol. i of this work.

† Celakovsky eventually held that the ovuliferous scale represents the vegetatively-developed outer integuments of the ovule.

as to the nature of the double scale in Abietineæ, Cupressineæ, *Cryptomeria*, *Taxodium*, and *Glyptostrobus*, yet argues that in *Agathis*, *Araucaria*, *Cunninghamia*, *Sciadopitys*, *Sequoia*, and *Athrotaxis* we have to do with a simple, not a compound structure. This view of his is based on the following facts: that the scale shows no obvious signs of its compound nature; and that in *Sequoia sempervirens*, which bears no close relationship to *Taxodium*, he observed androgynous cones in which some of the scales bore pollen-sacs on the lower and ovules on the upper surface, while other scales, similar in all respects to the ordinary pollen-sac-bearing scales, bore ovules on their upper surface, this fact proving that there is but a single scale present. But the probabilities are that in an abnormal cone of this sort in which the nutritive conditions were very much disturbed, the true male scales might very easily come to bear ovules; for we know many cases of ovuliferous stamens. Again, Velenovsky does not take into consideration the fact that Engelmann, in America, found a proliferated cone of *Sequoia* which clearly exhibited the compound nature of the scale. And it is probable that *Sequoia* is sufficiently nearly allied to *Taxodium* to warrant the position that the structure of the ovuliferous scale in each must be identical. In *Taxodium*, *Cryptomeria*, and *Glyptostrobus*, A. Braun found an axillary bud replacing the scale.

Velenovsky is most likely misled by the extreme intimacy of the union of the two scales to which the apparent simplicity of the double scale is doubtless due. Again, the anatomical structure of the scale of, e.g. *Araucaria*, with its upper series of inversely-orientated vascular strands, is so similar to that of the Abietinean scale as to suggest that the two are similarly constructed.

Although the other views as to the nature of the ovuliferous scale have not all to do with abnormal axillary branching, they may be introduced while this subject is being dealt with.

Baillon regarded the scale as of axial nature from the fact that during the early development of the cone it arises as a simple papilla in the axil of the "bract," not recognizing the fact that structures may be congenitally modified, the early stages through which the present structure has passed in the phylogenetic history not being represented in the ontogenetic development. Schleiden, also relying on the mode of development, held the scale to be an axial placenta.

Strasburger also held that the ovuliferous scale was of the nature of an axillary shoot; he regarded it as a kind of flattened axis or disk, chiefly on account of its late development compared with that of the ovules; the abnormal structures above cited he regarded as the result of the struggle waged between two opposing forces, viz., the vegetative development of the cone and the normal formation of reproductive organs, in which the former had for the time being overbalanced the latter. This position, however, Celakovsky shows to be perfectly untenable; for it is impossible for an organ belonging to one morphological category, such as an axis or disk, to become transformed into those belonging to another category, such as the foliar appendages of an axis.

Masters maintained that the ovuliferous scale is a half-cladode, *i. e.* an axial enation from either the bract or the axis of which the lower or outer portion has become abortive (*cf.* C. de Candolle's 'Théorie de la Feuille'). This view cannot be said to have found any support.

Just as Schleiden and Baillon followed the developmental method, and Celakovsky and others the teratological and comparative, so Van Tieghem followed the anatomical method in the endeavour to solve this problem. His idea is that the seminiferous scale in all Coniferæ represents the first and only leaf of an axillary branch, though he suggests the possibility of its being really two fused leaves. His view is based on the course and orientation of the vascular bundles

from the axis into the scale. It is doubtless very useful to have these anatomical data furnished for us, but to rely upon them as the sole criterion for explaining the phenomenon in question is decidedly unsafe, to say the least of it, *e. g.* we know that in all Coniferæ an axillary shoot always bears a pair of opposite leaves and not a single leaf.

Then there is the view of Sachs and Eichler that the ovuliferous scale is a ventral outgrowth from the open carpel (the "bract") of the nature of a placenta or ligule; in the Cupressineæ, Taxodineæ, Podocarpeæ, and *Agathis* no differentiated ventral outgrowth exists, but the scale as a whole represents a carpel.

Eichler's explanation of the abnormalities was this: that the pressure exercised by the axillary bud arising between the seminiferous scale and the axis of the cone was the agency responsible for the splitting of the scale into two parts and the wide separation of these into the positions which they occupy, one on either side of the axillary bud. But Celakovsky says that this theory will not hold good when it is found that the splitting of the scale frequently occurs when the axillary bud is suppressed or exceedingly reduced, and also when it arises on the anterior side of the seminiferous scale; a fact which is fatal to Eichler's placental or emergence-theory, which is, however, best refuted by the continuous, gradual transitions which occur in the abnormalities between the seminiferous scale and the first leaf-pair, plus the anterior leaf, of the axillary bud. And further, if this view of Eichler's be correct, what has become, he asks, of the first transverse leaf-pair of the bud, which should occupy the position taken up by the separated parts of the seminiferous scale?

Delpino and Penzig put forward a theory which is strikingly ingenious and original. According to them the ovuliferous scale represents two basal lateral lobes of the carpel ("bract") which have become folded over on to the upper face of the carpel and united by their margins to form a single leaf-like organ bearing the

ovules on its upper surface, *i. e.* the lower face of the carpellary lobes. When an axillary shoot arises between the "bract" and the ovuliferous scale it splits the latter into its two component parts, causing these to resume their original orientation as lateral lobes of the "bract," and also carries them up attached to its axis as apparently the first transversely-placed pair of leaves thereof. It is owing to the position assumed by them that the real first pair of the axillary shoot comes to assume an antero-posterior position. When the shoot arises between the ovuliferous scale and the cone-axis, the two halves of the scale have their lower surfaces directed towards the axillary shoot, a fact which Penzig (who is responsible for the elaboration of this theory) regards as fatal to Braun's theory of the scale. But it does not seem that this conclusion necessarily follows; for this particular position of the axillary shoot implies its imperfect development, so that its first two leaves still retain in part (as shown by their orientation) their character as halves of a seminiferous scale. The fact observed by Velenovsky of several fleshy ovuliferous scales succeeding and completely resembling the two ovuliferous scales on the axillary shoot, Penzig explains by the other fact that in many cases the character of an abnormally-formed phyllome is determined by that of the normal phyllomes in juxtaposition to it; he cites instances in abnormal blooms of *Antirrhinum* and orchids in support of this.

While admiring the clever hypothesis of Delpino and Penzig, one feels inclined to regard it as somewhat far-fetched.* Braun's theory must be held to be much more natural and easy, and that which, on the whole, explains the facts the best.

If Braun's view is correct, the female cone of the Coniferæ is an inflorescence, and the foliar organs in whose axils the abnormal shoots arise are bracts, while

* The far-fetched nature of Delpino's theory is seen more clearly when he comes to apply it to an explanation of the "double needle" of *Sciadopitys* and the ovuliferous organ of *Ginkgo*, though in so doing he, of course, exhibits his consistency of view.

the ovuliferous scale is the highly-modified equivalent of a Gymnospermous flower.

The production of leafy shoots in the axils of the involucre bracts of the Compositæ is not nearly so common as that of secondary heads in that position; but it occurs sometimes in *Bellis*. Clos mentions the formation of leafy shoots in place of the florets, or some of them, in the wormwood (*Artemisia campestris*).

Of shoots axillary to *sepals* there was observed an enlarged and more or less virescent flower of a carnation which had seven sepals from the axil of each of which arose a shoot bearing a dense aggregation of bract-like foliar organs.

A very frequent abnormality in the pear is that of the formation of a longer or shorter shoot, bearing a second pear at the end, in the axil of a small leaf borne on the surface of the ordinary "fruit" (fig. 67). Now, this small leaf is probably a sepal whose base, unlike that of the other sepals at the top of the "fruit," has not become adnate to the ovary along the whole length of the latter; such a shoot

must be adventitious in the axil between the sepal and the ovary. On the view (not here supported) which regards the pear-fruit as an axis, the position is more natural, namely, that of an ordinary axillary shoot.

In the very striking phenomenon described and figured by Knight, viz., that of the production of potato-tubers in the axils of the sepals of *Solanum*, the flower showed a central fruit with one or more potatoes around it.

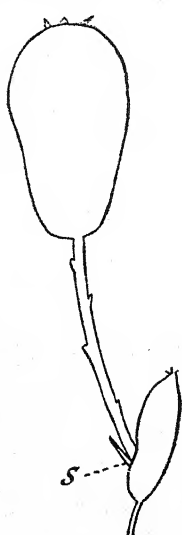


FIG. 67.—*Pyrus communis* (Pear). Shoot, bearing a terminal pear, arising in "axil" of a sepal on the primary pear. (Semi-diagrammatic.)

Small, apparently branched, buds have been observed in the axils of the sepals of the sweet violet (*V. odorata*). A flower of the Indian cress (*Tropæolum majus*) was seen in the axil of a foliaceous sepal.

Vegetative proliferation from the axils of the other organs seems to be rare.

As an instance of the kind in relation to *carpels*, a strawberry (*Fragaria vesca*) had a leafy shoot bearing a flower at its apex, arising from the axil of one of the tiny achenes (representing a single carpel) seated on the fleshy receptacle.

Masters suggests that the terminal leafy shoot sprouting from the virescent flower of *Trifolium repens*, often ensheathed as it is by the virescent carpel at the base, may, in reality, perhaps represent a shoot axillary to this single terminal carpel. It seems, however, more likely that the proliferating axis of the flower has displaced the normally terminal carpel into a lateral position. From the very fact that it is solitary the carpel inevitably comes to occupy a terminal position, and Payer, in his work on floral development, describes it as arising "in the middle of the receptacle." This being so, it is impossible for a shoot to arise in its axil. Therefore this interpretation of the phenomenon cannot be accepted.

CONCLUSIONS ON PROLIFERATION.—Having now given illustrations of the principal types of "proliferation" or "prolification" which occur amongst plants, it remains to consider the meaning of the phenomenon. There is little doubt that, like the majority of other abnormal phenomena, that which we call proliferation is the expression of the tendency, under, as a rule, certain unfavourable conditions of climate, nourishment, or the influence of parasitism, to revert to a primitive or ancestral habit or structure. In modern days, under the influence of a more extended acquaintance with the facts of comparative morphology and of fossil botany, many have been led to perceive what an enormous rôle

the process of reduction, in the guise of an advanced type of simplification, has played in the course of the evolution of modern vascular plants.

If we cull a particular instance from our knowledge of the configuration and habit of the seed-ferns of the Carboniferous epoch and the method by which they, through the process of reduction and simplification, from an excessive complexity of their reproductive apparatus, gave rise to that of the Cycads of the Mesozoic period; and if we consider how greatly the cone of these Mesozoic Cycads resembles in general conformation the "flower" of an Angiosperm; we shall feel that a "flower" is, after all, merely the final stage in the evolutionary transformation of a leafy shoot of complex organization such as we find in the Pteridosperms. A sepal, a stamen, and a carpel have probably each been derived during the course of evolution from a large foliar organ, whether green and assimilating or not, of complex structure. The receptacle or floral axis has likewise in the course of ages been excessively abbreviated owing to complete or almost complete extinction of the internodes between the various floral leaves. All these changes have resulted in the characteristic modern structure which we term a "flower," *e. g.* the tulip.

When, as under the stimulus of excessive nourishment, the normal balance of the structure is upset, which condition is a kind of disease, there appears to be a tendency for it to revert to a state which can only be termed ancestral, but ancestral merely in the sense that two changes take place, namely, an excessive elongation of the axis in which the internodes develop, and secondly, the modification of the various floral leaves into foliage-leaves. The flower, in other words, frees itself from the bonds of contraction and condensation in which it has so long been held, and attains to a reminiscence of bygone ages in which its ancestors revelled in the luxuriance of a more extended scope of shoot and leaf. A reversion, be it noted, only

in this way and sense, for the type of shoot and leaf developed in the proliferated flower will, of course, be characteristic of the plant of the present day and similar to that of its own normal vegetative parts. In a proliferated flower, in its extreme form, all the four kinds of floral leaves—sepals, petals, stamens, and carpels—become changed into foliage-leaves like those of the vegetative part of the plant, and where “inferior” ovaries occur, as in the rose, they vanish entirely. The axis also branches very often, which is another aspect of the ancestral complexity.

The great majority of people would probably agree that highly congested structures like the spike of a plantain or a grass, the capitulum of a daisy or scabious, the catkin of a hazel, are not primitive structures, but, on the contrary, highly modified from some much laxer, larger, and more complex type of inflorescence. Hence it would be easier for the sceptic to admit that the abnormal proliferated forms of such structures as have been above described are giving some indication by their change of what the ancestral inflorescence was like.

The matter becomes much more difficult when we have to deal with structures so highly modified in their normal condition that we can no longer tell to what morphological category they belong, *e. g.* the ovuliferous parts of Coniferæ. Yet few would deny nowadays that the cones, both male and female, of Coniferæ represent extremely congested and reduced structures; hence any process of branching which is set up in them during the course of abnormal modification is, on the face of it, as likely as not, to represent a tendency towards reproducing a more ancestral condition, however far back this is to be sought.

But it cannot be too strongly insisted upon that in most, if not all, of these cases we have not to do with a direct reversion to the condition of a particular type which has existed in the past in this particular form; but the proliferations are to be considered as the

process by which the structures concerned become freed from the restraint of congestion and reduction into which they have been brought in the course of evolution. Hence we may truly say that this process is a reversionary one.

As we should expect, and as Masters appositely points out, proliferation is most frequent, on the whole, in plants or groups whose inflorescences or whose flowers have become less severely congested and reduced in the course of evolution, namely, in those with indefinite inflorescences, or with flowers whose axis is, in one part or another, normally somewhat elongated, *e. g.* the inflorescences of Cruciferae and Leguminosae, the feræ, Primulaceae, and Caryophyllaceae.

And axillary proliferation tends to be more common in groups some of whose members are normally branched in the inflorescence.

There are cases of proliferation which we may regard with certainty as representing the exact condition of the ancestry of the plants concerned, as in the caulescent abnormality of the common primrose; for the inflorescences of the vast majority of this order are of this caulescent type. On the other hand the extreme forms of floral proliferations are obviously new structures, unheard of in the immediate ancestry of the plants affected. In other instances where we cannot presume with certainty that the proliferation is a reversion to a character in the immediate ancestry, yet when we find that the abnormal feature occurs as a perfectly normal one in other closely allied members of the group, it no longer assumes a strange and unnatural appearance, and in such cases the reversion theory is probably much more applicable than any other. For example, the abnormal branching of the spike in *Plantago major* and *P. lanceolata* finds its counterpart in the normally branched inflorescence of such species as *P. Cynops* and *P. Psyllum*.

The abnormally-branched inflorescences of the ryegrass (*Lolium*) are but reproducing a character which

predominates in the majority of the Gramineæ, and thus may almost certainly be regarded as a reversion to the condition of the immediate ancestry.

The disappearance of the cupular formation and the "inferior ovary," as in the abnormal roses and pears, can only be considered as a reversion to the condition of those Rosaceæ in which cupular structures do not exist, and these are, on morphological grounds, doubtless the more primitive.

The result of this study is the conclusion that proliferation represents in two senses a reversion, and is derived from a consideration of the following facts: (1) that the most ancient type of reproductive axis from which our "flower" has been derived was a complex leafy shoot; and (2) that in the more immediate ancestry of the various recent forms, the complex paniculate inflorescence and the flower with elongate receptacle were predominant and gave rise to all the later more congested types.

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2. FORKING AND FASCIATION.

The term “fasciation” has already been defined and the phenomenon explained as it affects vegetative axes; it is essentially the same phenomenon where it affects inflorescences and flowers, and what has been said about it on earlier pages of this work will apply equally well here.

1. THE INFLORESCENCE.

The phenomenon of Forking and Fasciation, as in the stem, consists in its simplest form of a simple dichotomy or forking of the axis, the two resulting branches of which may be either equal or unequal. This was observed to be such a frequent occurrence in the inflorescences of such a number of specimens of the cherry-laurel (*Prunus Lauro-cerasus*) in Kew Gardens, being dependent merely on the vigour of any particular raceme, the more vigorous and stouter generally forking, the less vigorous remaining undivided, that the boundary line between so-called “normal” and “abnormal” inflorescences became completely obscured. Just the same may be said of the inflorescences of *Liriope* and of the garden hyacinth. Pl. XXXII shows a good instance of forking

in the lupin. Female cones of *Welwitschia*, showing various stages of forking, were collected by the writer in Damaraland.

As in the stem, the more complex type of forking by which an exceptionally robust and vigorous inflorescence tends to divide at the apex, after broadening into a flattened structure below, is styled *fasciation*. Magnus described a fasciated inflorescence of the mountain scorpion-grass (*Myosotis alpestris*) of especial importance as bearing upon the morphological nature of the inflorescence of Boraginaceæ. Braun, Schimper, Wydler, and Celakovsky, as a result of comparative morphological studies, held it to be a sympodium, whose first-formed flower was terminal. Kaufmann, Kraus, Warming, Goebel, and others, relying on the utterly misleading data of the ontogeny, considered it to be a monopodium, with all the flowers as lateral branches. Now Magnus points out that, if this last view is correct, the fasciated axis of the inflorescence should bear the flowers singly in a lateral position; whereas, if the sympodial theory is correct, the fasciated axis should bear a terminal flower and a number of subsidiary cymes laterally in the axils of the leaves. This is actually the case. A quite remarkable example of the efficiency of a teratological phenomenon for solving a morphological problem!

The abnormal inflorescence shown in Pl. XXXIII, fig. 1, is best regarded as a case of fasciation rather than of fusion, and that for two reasons: (1) dissociation of parts seems to be proceeding, as shown by the undoubtedly fasciated rays into which the fasciated portion of the umbel divides, and by the presence of one-flowered pedicels in different parts of the inflorescence; (2) the peduncle of the inflorescence is fasciated. Thus the phenomenon probably consists of fasciation of a single primary ray, and this would necessarily cause a decrease in number of the normal rays, thus giving rise to the appearance of fusion in order to account for the diminished number.

There may be mentioned a quite distinct type of fasciation, which involves suppression or transformation of the flower itself due to great vegetative development of the pedicel. In the ash (*Fraxinus excelsior*) there is a disease, due to the mite *Phytoptus fraxini*, which causes fasciation of the tips of the pedicels while the flowers appear as curious swollen knobs.

The same kind of thing, in which, at the same time, the whole inflorescence becomes greatly hypertrophied, involving very copious branching of the pedicellar system, and in which the flowers are completely sup-

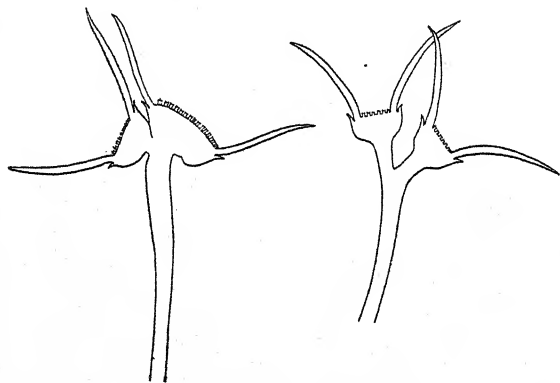


FIG. 68.—*Chrysanthemum segetum* (Corn Marigold). Bifurcation of capitulum, showing two stages. (Diagrammatic.)

pressed, has given rise to the variety of the cabbage known as the cauliflower (*Brassica oleracea botrytis*).

The capitulum or "head" of a chrysanthemum may either simply bifurcate more or less completely (fig. 68), or it may fasciate, forming a flattened more or less transversely-elongated head, in which no division into separate heads is at all manifest, the disk-florets being continuous right across (fig. 69); and, under such circumstances, it is usually, owing to inequalities of growth in the stalk below it, contorted and bent in more than one plane in a most complicated manner. The central continuous area of disk-florets

corresponds to the transversely-extended, continuous pith of a fasciated vegetative stem. Such a fasciated inflorescence is one in which the tendency to subdivide has become but partially and incompletely manifested. Conditions more advanced in this direction are often observed in such capitula, in which the individualization into separate heads is becoming marked, and there are all degrees of that condition. Constrictions appear



FIG. 69.—*Bellis perennis* (Daisy). Fasciated peduncle and capitulum and normal daisy at side for comparison. (W. H. Hammond, photo.)

in the capitulum by which the ray-florets arise ever nearer and nearer the centre, until ray-florets and bracts may extend completely across the head as the division into secondary heads becomes more pronounced, until, finally, these heads become completely individualized, each with its own involucre, and either sessile and crowded together, or stalked and more distant.

Before leaving this subject of fasciation of the inflorescence there is one other matter that may be referred to. In many strongly-fasciated terminal

inflorescences there is, if not a complete absence, a much greater dearth than is normally the case, of lateral inflorescences. The two phenomena are thus obviously correlated, the one being the result of the other. Yet, bearing in mind the definition of "fasciation" given in an earlier section, it would, on this definition, not be correct to say, as, for example, in the instance frequently seen in the spear thistle (*Carduus lanceolatus*), that the fasciated terminal head was due to fusion of the lateral heads with the terminal one, for there is no evidence of any such fusion. Rather we should say that the fasciated head is the equivalent of the two categories of heads (terminal and lateral). The main head, with the axis bearing it, has, for one cause or another, started in a condition of excessive robustness and vigour, and this has involved the absence of sufficient superfluous vigour and nourishment for the formation of the normal number of lateral heads; hence, in one sense, it is true that these have become congenitally absorbed or fused into the main head and tend to become separated out again at the apex (so to speak).

It is this primary congenital "absorption" of individuals which might, under other conditions of the environment or of the plant's constitution, have been formed separately, together with their subsequent separation, or partial separation, at the apex of the structure so formed which gives rise to the phenomenon of fasciation wherever, in the vegetable kingdom, it may be found. For example, it might happen that an ovum of abnormal development, equal, perhaps, in size to two ordinary ova, is formed in the embryo-sac. If this ovum divides completely into two, twin-embryos are the result; if it does not so divide the result of fertilization would be an abnormally robust embryo producing a plant with a tendency to fasciation. The idea of "fusion" is only permissible here in the sense that, where a single abnormally large ovum was formed, two ova of normal size might have been formed. The

same conclusions may be drawn with regard to the fasciated capitulum of *Carduus*. Or, again, in a very moist season, rapid development at the apex of the root-stock of a perennial plant might induce formation of a particularly vigorous shoot, which is the equivalent of two or more shoots, in this sense, that the tissue-matrix from which it arises within the root-stock might, at the period of its development when it is about to emerge as a completed bud, divide into two buds producing the appearance of two shoots, distinct from the beginning; or it may not so divide, and would then produce a fasciated shoot, or one with a tendency thereto.

RING-FASCIATION.—There is a second method whereby individualization of the secondary heads is attained—viz., by “ring-fasciation.” The result of this is the formation of two or more heads. The phenomenon here is not quite the same as ring-fasciation in the vegetative stem; in the latter it is evidently due to terminal invagination of the tissues in a vertical direction; in the case of the capitulum the phenomenon is brought about by lateral invagination in a horizontal direction, whereby the involucre reaches and occupies the centre of the head while continuous with its normal external portion. In some instances there may be absolutely no sign of any such invagination, the involucre and ray-florets appearing congenitally from the commencement of the development in the centre of the disk, the involucre being innermost and its bracts having their dorsal side directed towards the centre, these being succeeded in the outward direction by ray-florets, and the disk-florets being, therefore, sandwiched all round between the normally- and abnormally-placed ray-florets. This phenomenon represents one stage, isolated and congenitally formed, in the division of the capitulum into two. The lateral invagination above-mentioned represents another isolated stage. Still another stage is seen, representing a more advanced condition of division, where (to describe it in one of

various ways) an invagination takes place on opposite sides of the head, the two meet in the centre, and thus completely divide the head into two.*

A curious form of "double" daisy (*Bellis perennis*) was seen which may be attributable to ring-fasciation. The main capitulum consisted of three to five separate small heads bunched together, but there was in this case a common involucre surrounding the whole.

A dahlia was also seen which had a triple head within a common involucre. "Ring-fasciation" thus appears to be nothing more or less than a process whereby forking of the capitulum is attained.

2. THE FLOWER.

a. ORDINARY FASCIATION.—A forked or fasciated flower exhibits just the same appearance and phenomena as a fasciated or forked capitulum of a Composite. All the same degrees and stages are met with, from that in which the diameter of the flower is merely increased beyond the normal, either symmetrically or in one plane only (Pl. XXXIII, fig. 2), a good example of which was seen in a rose, to that in which two or more perfectly distinct and separate flowers are formed. Good instances of the first degree of fasciation are afforded by the auricula and polyanthus, types of what occur in many other flowers, in which the flower becomes enlarged, and the number of members in each whorl increased, so that the abnormality ranges from 6-mery in the least modified flowers to 25-mery in flowers showing the greatest degree of fasciation. These flowers represent incipient stages in the differentiation and individualization of two or more distinct flowers (fig. 70). So that, remembering that the normal flower is 5-merous, our abnormal 6-merous flower may be regarded as the equivalent of $1\frac{1}{5}$ normal flowers, the 25-merous flower as the equivalent of five normal flowers. Dr. E. J. Salisbury

* Reference to the diagram of this phenomenon, as it occurs in the flower, given on a later page, will make its nature clear.

sent interesting statistics concerning flowers of the primrose (*P. vulgaris*); e.g. one flower had eight sepals, seven petals, seven stamens, and seven carpels.

In some flowers, as in many auriculas, the increase in number is the same in every whorl. In most fasciated flowers, however, there is great variation in this respect. For instance, in a flower of crocus, received from Dr. Stapf, there were ten perianth-leaves (there would have been twelve if four members of the

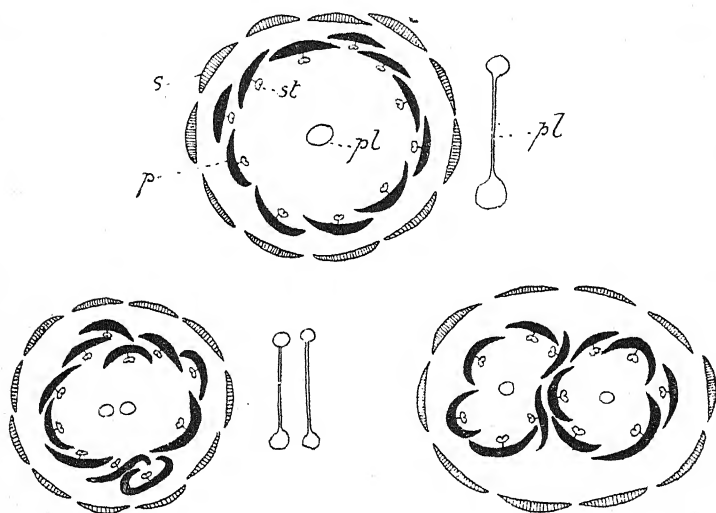


FIG. 70.—*Primula vulgaris* var. (Polyanthus). Diagrams of three flowers showing three stages in the bifurcation of a flower. s, sepals; p, petals; st, stamens; pl, pistil.

outer whorl had not each fused with a member of the inner whorl), six stamens, two styles, and corresponding sets of stigma-lobes, i.e. six carpels. A flower of *Cattleya intermedia* had four sepals (three of ordinary size and one double); nine petals, of which three were labella, while one of the other petals is semi-labelliform; there were three coherent columns, though the stigma and andrœcium of each were individualized. This flower is evidently the equivalent of three flowers. In a flower of *Odontoglossum crispum*

recently examined there were four sepals, the uppermost (morphologically anterior) being forked; there were six petals (of which two were labella); the column was double below, triple above. Here we see more than the equivalent of one flower (for there are six petals and a double or triple column), but not quite the equivalent of two flowers (for there are only four sepals).

A most interesting case was that of a polyanthus received from Dr. Salisbury. There were three fasciated flowers on the same plant; of these one had eleven sepals, eleven petals, nine stamens, and one ovary about twice the normal size and probably composed of about ten carpels; another flower was similarly composed as regards calyx and corolla, but there were eleven stamens and two distinct ovaries and stigmas, each of the normal size; in the third flower the fasciation had proceeded further, and advanced stages of division into two flowers had set in: there was a single common calyx of eleven sepals, but otherwise two distinct flowers closely adpressed together, each of six petals; one with five, the other with six stamens; and each with a normal ovary (fig. 70.)

All degrees of separation into distinct flowers are seen in the various fasciated flowers which are so frequently found. In that of a Canterbury bell (*Campanula Medium*) examined, the transversely-elongated flower was single, but was the equivalent of four flowers, about twenty members in each whorl being present; in another flower, also the equivalent of four, two had become separated out. In a flower of the pheasant's-eye (*Narcissus poeticus*) there was the equivalent of seven flowers which had become nearly individualized, though the members of the different whorls did not quite reach the requisite numbers; *e. g.* of the row of seven ovaries, all coherent, the one at each end was 3-locular, an adjoining one was 3-locular, but the remaining four were 2-locular and much laterally compressed (fig. 71). A *Cypripedium* was examined, of which fig. 72 shows the

composition; an interesting feature of it is the occurrence of a petal on the side opposite the labellum.

Then there is the case of the abnormal sweet

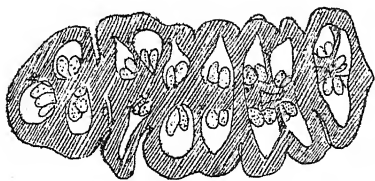


FIG. 71.—*Narcissus poeticus* (Pheasant's-eye). Fasciated ovary, the equivalent of seven ovaries.

pea (*Lathyrus odoratus*) described in the 'Gardeners' Chronicle,' which is an excellent instance of multiple forking (=fasciation) within a common calyx and part of a common corolla; there was present the equivalent

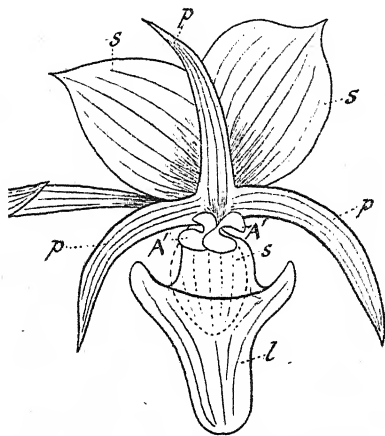


FIG. 72.—*Cypripedium callosum*. Incomplete bifurcation into two flowers; an extra posterior sepal; a posterior petal; and two staminodes. Possibly a case of synanthly. *s*, sepals; *p*, petals; *l*, labellum; *A*, staminode.

of four or five flowers, that number of pistils and of stamen- and petal-groups being present.

In some abnormal male cones of *Welwitschia* collected by the writer in Damaraland several flowers each con-

tained within its perianth three or four flowers of the second order, some of which were normal, others abnormal.

Under the head of the inflorescence was cited the interesting phenomenon in which a fasciated terminal capitulum (e. g. in *Carduus lanceolatus*) was brought about by the absorption into it, as it were, of some of the lateral capitula. A precisely similar type of

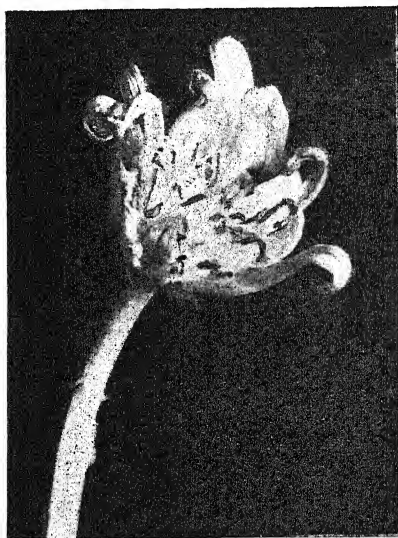


FIG. 73.—*Scilla nutans* (Wild Hyacinth). Fasciated terminal flower; peduncle entirely devoid of flowers.

fasciation occurs in the flower. An abnormal inflorescence of the wild hyacinth (*Scilla nutans*) was received in which the racemose habit had entirely vanished; replacing it was a long bare stalk bearing a large, peloric, fasciated terminal flower (fig. 73) consisting of great numbers of stamens and perianth-leaves. It was obviously the equivalent of several flowers of the raceme. The bareness of the stalk below it was due to the disappearance of the lateral flowers and their

subtending bracts; but half-way down the scape was a petaloid elongated bract with a tiny blue petal (sole vestige of a flower) in its axil.

This last fact seems to show that the disappearance of the lateral flowers is due, not to synanthly, *i. e.* their fusion together to form a single compound apical flower, but to the fact that the developmental energies and nourishment have been concentrated at the apex of the whole inflorescence, *i. e.* in the uppermost flower, thereby preventing the proper, or any, development of the lateral flowers and their bracts.

If this abnormality is to be explained by supposing that all the lateral flowers have fused with the terminal one of the raceme, then the presence of the tiny blue petal half-way down the scape must be accounted for by supposing that part of the flower originally in that position has been carried up and become fused with the terminal one, and part of it has been left behind. But this would be a far-fetched conception of a case without known parallel.

A very similar abnormality occurs in the foxglove (*Digitalis purpurea*). The large, terminal, peloric flower is the equivalent, and is due to the "absorption" into it, as it were, of several of the uppermost flowers of the raceme (Pl. XXXIV); as in the *Scilla*, rudimentary flowers in the guise of single, tubular petals, occur in the axils of some of the uppermost bracts.

Hence neither of these two phenomena can be ascribed to "synanthly"; it seems best to regard the large terminal flower as a single, not a compound, structure. There is a tendency, in the upper part of the raceme, towards the rapid and vigorous development of a large terminal flower, and, in the foxglove, the lateral flowers are imperfectly formed and congested towards the top, while in the *Scilla* they are not formed at all save for a single isolated petal, all the nutriment being carried up to the apex of the inflorescence. There is no real evidence in either case of actual fusion of two or more distinct flowers.

Fasciation in "Fruits."—The strawberry (*Fragaria vesca*) affords one of the best-known instances of fasciation; most of the "fruits" exhibited at shows are examples of the fasciated receptacle of the flower,

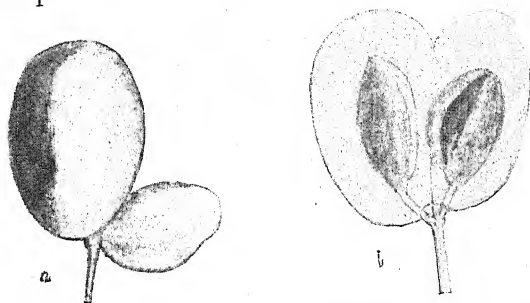


FIG. 74.—*Prunus domestica* (Plum). Double fruits. *a*, second fruit almost separated; *b*, longitudinal section of fruit showing two distinct stones. (G. S. Saunders.)

with a differentiation of two apices, one at each end, representing the incipient division into two distinct "fruits." Or the "fruit" may be trifid: the equivalent of three fruits, branching thus in two planes.

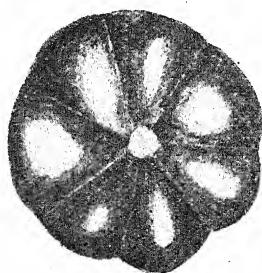


FIG. 75.—*Vitis vinifera* (Grape). A sevenfold fruit. (After Turpin.)

Fasciated or dichotomous fruits of cherry, plum (fig. 74), cherry-laurel (*Prunus Lauro-cerasus*), and grape, are common; in the first three the fasciation is usually of two, in the grape it may be of as many as seven parts arranged in a circular plane (fig. 75). Fasciation is common in many other fruits, *e. g.* the gourd (fig. 76), gooseberry, orange, and apple.

The quasi-paradoxical nature of fasciation (a compromise between coherence and separation) as illustrated in the case of a fruit, is well brought out by some lines in "A Midsummer Night's Dream" which, on the precedent of Masters, may here be quoted:

"A double cherry, seeming parted ;
But yet a union in partition,
Two lovely berries moulded on one stem."
—*Mids. Night's Dream*, Act III, Sc. 2.

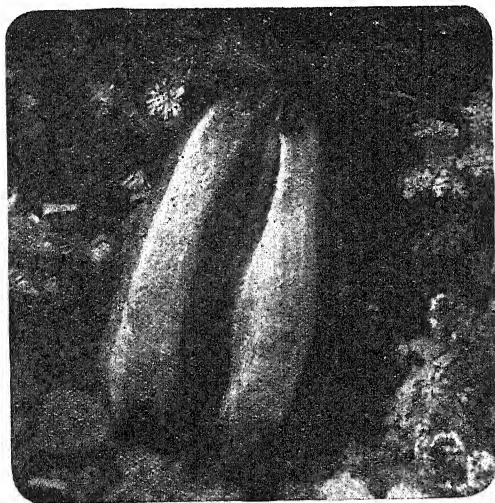


FIG. 76.—*Cucurbita Pepo* (Vegetable Marrow). Twin or fasciated fruit.
(E. J. Salisbury photo.)

b. RING-FASCIATION.—This is merely a stereotyped stage in the dichotomy of the flower, and is brought about as follows. A lateral constriction occurs, involving an invagination of the outer tissues or floral leaves; if this were to proceed half-way across we should get the condition as stereotyped in frequent abnormal capitula as in that of a *Pyrethrum* observed. If the constriction were to continue completely across the organ, or were met by a similar one approaching from the opposite side, then simple division of the

organ into two would occur. But what has clearly happened in the past is that the invagination, on reaching the centre, widened out, the gap connecting this wide, central portion with the exterior then became closed, and the peripheral tissues, florets or leaves, of the organ once more continuous, so that a circular space was left in the centre with the orientation of all the parts lining it, of course reversed. This condition we find stereotyped in the various cases of "ring-fasciation" met with. It appears congenitally as such

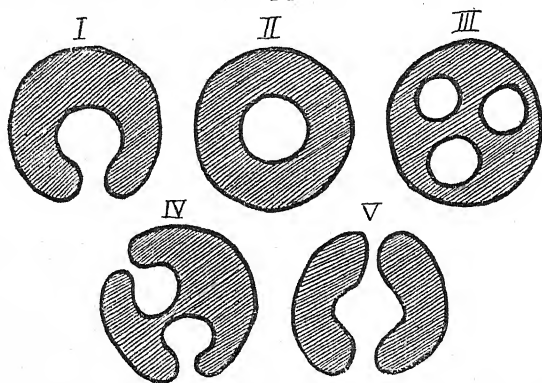


FIG. 77.—Diagrams of "ring-fasciation." I. A single lateral invagination. II. Later stage, showing central cavity which is lined by bracts and ray-florets. III. Three cavities formed by three invaginations (= stage towards trifurcation. IV. Two invaginations. V. Bifurcation caused by two invaginations, from opposite points, meeting in centre.

with, as a rule, no indications as to how it was brought about. Intermediate stereotyped stages connecting this one with actual forking have not been observed, although it is highly probable that such occurred in the past. If ordinary dichotomy were to succeed this stage, a connection between the central space and the peripheral part of the structure would take place on two opposite sides. Multiple dichotomy would result from a number of invaginations, instead of one or two only, which would meet and fuse in the centre (see the diagrams, fig. 77).

The phenomenon of "ring-fasciation" is frequent

amongst flowers. Perhaps the best-known case of this is seen in the mountain scorpion-grass (*Myosotis alpe-*

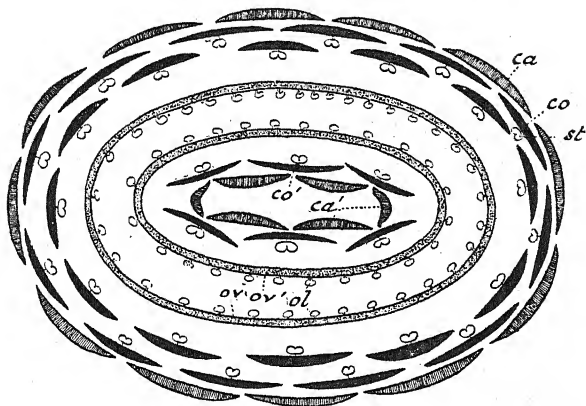


FIG. 78.—*Myosotis alpestris* var. *Victoria* (Mountain Scorpion-grass). Diagram of ring-fasciated flower, showing also pleiotaxy of the normal corolla. (Diagrammatic.) *ca*, calyx; *ca'*, inverted calyx; *co*, corolla; *co'*, inverted corolla; *st*, stamen; *ov*, ovary; *ov'*, inverted ovary; *ol*, ovule.

tris var. *Victoria*), affecting the terminal flower of the inflorescence. The abnormality is exactly the same

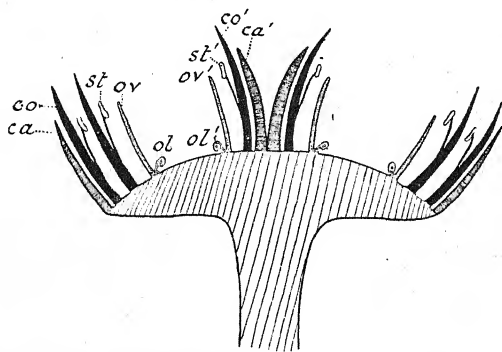


FIG. 79.—*Myosotis alpestris* var. *Victoria*. Longitudinal section of ring-fasciated flower. (Diagrammatic.) *ca*, calyx; *ca'*, inverted calyx; *co*, corolla; *co'*, inverted corolla; *st*, stamen; *st'*, inverted stamen; *ov*, ovary; *ov'*, inverted ovary; *ol*, ovule; *ol'*, ovule of inverted ovary.

as that above described for the capitulum of *Chrysanthemum* so that the account need not be repeated here.

But in some cases there are, instead of one, two centres in the whole flower around which the floral members are arranged in reverse order and with inverse orientation; in such we have the equivalent,



FIG. 80.—*Rosa centifolia* (Garden Rose). A "rogue" rose (afflicted with a kind of ring-fasciation).

not of two, but of four flowers in the whole structure. The diagrams given of the commoner case sufficiently explain themselves (figs. 78 and 79). It may be mentioned that sometimes three distinct normally-constructed flowers become separated out.

An instance in which an indefinite number of flowers is so formed is perhaps afforded by the "rogue" roses so common in gardens. The carpels become enlarged, virescent, and superior in position, and assume the rôle of a common calyx for the secondary flowers which are formed all around on the outside of them, this calyx becoming, for the purpose, orientated in an inverse direction. The strong centrifugal growth taking place causes many of the secondary flowers to be pressed outwards and completely inverted (figs. 80 and 81). The calyx, corolla, and many of the



FIG. 81.—*Rosa centifolia* (Garden Rose). Longitudinal section of a small portion of a "rogue" rose, showing one of the inverted secondary flowers (*fl.*). *st.* and *cp.* stamens and carpels of primary flower.

stamens of the mother-flower remain unaltered. On sectioning the stalk just below the flower there was found a ring of bundles with inversed orientation surrounding a central cavity lined by an epidermis, *i. e.* the typical structure of ring-fasciation; at the periphery of the pith were other small inverted cylinders representing probably the secondary dichotomies.

There is a curious condition of the flowering currant (*Ribes sanguineum*) in which each flower breaks up into a number of closely-compacted flowers, the parts of each of which are greatly multiplied and the majority changed into small petaloid organs. It may come under this heading.

CONCLUSIONS ON FASCIATION.—Having already fully discussed the subject of "fasciation," much more need not here be added. What remains still to be said has reference to a question of terminology. Having reached the conclusion that "fasciation" really represents a division and not a fusion, it becomes impossible to accede to the old-fashioned view of classing all these cases under "synanthly" or "syncarpy," for these terms denote that the phenomenon is always due to fusion. It is quite likely that some cases of polymery in flowers are due to synanthly; but evidence of this can only be forthcoming when it is shown that the phyllotaxy on the stem is disturbed and that thereby flowers have actually become approximated and fused. There is no evidence that this was so with any of the flowers above described. Fasciation in all these cases, as in that of a fasciated stem, must be due to extension and subdivision of a single individual.

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3. DISRUPTION.

The structure of the normal maize-cob is the result of a phenomenon which would seem to be unique in the vegetable kingdom.* It consists of the fusion of numerous spikes with flattened rachis, each bearing two rows of female spikelets, to form the thick female inflorescence usually termed the "cob." This cob is often spoken of as a "fasciation," but inasmuch as it is obviously not, as all fasciations are, a single branching structure, but a compound one, due to the congenital union of a number of branches of the same inflorescence, the abnormality about to be described must be placed under a distinct heading which may be termed "disruption." This consists in the appearance of the "cob" as a copiously-branched paniculate inflorescence, closely resembling, in its extreme form, the male inflorescence; and is due to the dissolution of the compound organ into its original separate parts. Blaringhem, by artificial torsion of the stem, induced the same phenomenon, which must certainly be regarded as a reversion to an ancestral condition in which the inflorescences of both sexes resembled each other, or in which both sexes were intermingled in one and the same paniculate inflorescence. Blaringhem regards it as a reversion to the type of inflorescence at present exhibited by the grass *Euchlaena mexicana* (Reana) which he considers to be in all likelihood the primitive wild ancestor of *Zea Mays* (Pl. XXXIX, figs. 13 and 14).

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* It is unique only as regards the fusion together of axes; the type of foliage obtaining in the Cupressineæ is due to the congenital fusion with the axis of the leaves which, in the juvenile or "Retinospora" condition, are quite free.

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4. POSITIVE DÉDOUBLEMENT.

This is a term borrowed from the writings of Celakovsky. When the tendency for an organ to divide becomes all-potent, overriding completely that which makes for unity, the result is the formation of two organs instead of one: this is *positive dédoublement*. It has been usually applied to the phenomenon termed by many authors “polyphyly,” viz., the increase in number of the members of a floral whorl. But it may equally well be applied to the phenomenon of “pleiotaxy,” or the increase in number of the whorls of a flower, and in this dual sense it will here be used.

The phenomena of positive dédoublement in the abnormal cases considered in the following pages may

be grouped under three main stages, each representing a further step backwards towards the ancestral condition: (1) increase in number of the members of a whorl; (2) increase in the number of whorls; (3) these two resolved into a spiral arrangement of the floral members. Nägeli was the first to point out that this arrangement is the most primitive and preceded the cyclic; Engler, on the other hand, maintaining that both are equally old.

As a type of a flower exhibiting this phenomenon the garden tulip (*Tulipa Gesneriana*) may be taken. Several kinds of polyphyly are seen in this flower: it may affect one, two, or three of the whorls only, the the others being normal; very often the whorl so affected is the pistil, as in flowers in which an extra carpel was added, giving the formula $K3 C3 A3 + 3 G^4$; in another flower there were six carpels, apparently all in one whorl; in another there were nine carpels, an outer of six, an inner of three, arranged in two whorls; in a flower of the wild tulip (*T. sylvestris*) the formula was $K4 C4 A4 + 3 G^3$; in one of *T. triphylla* $K4 C4$ (one petal half-staminoid) $A4 + 3 G^4$, in which all the whorls save one of the staminal whorls had been increased by one. In these examples we see irregularity and apparent lack of any clearly-defined method in the process of increasing the whorl-members. In other cases, however, the change takes place more uniformly, and in many instances as if governed by some fundamental law. In some flowers of the garden tulip there was an increase of one only to all the whorls except the pistil, which had two added to it: $K4 C4 A4 + 4 G^5$. A *Crocus* may be mentioned in which the number in each of the whorls was increased by one: $K4 C4 A4 G_4$; in another it was increased by two: $K5 C5 A5 G_5$, giving a structure like that of a typical Dicotyledonous flower. Buchenau describes exactly the same thing in *Lilium croceum*.

In the herb Paris the flower is normally 4-merous, at least in *P. quadrifolia* and other species. But 5- and

6-merous flowers are exceedingly common as abnormalities, and this condition is the normal feature in *P. polyphylla*, in which even 7-merous flowers are not at all uncommon. The 4- to 7-mery of *Paris* probably represents an older character than that met with in the flowers of other Liliaceæ.

But the most interesting cases are those in which an increase of one member occurs, not haphazardly, but with extreme regularity and system, viz., in every alternate whorl, the phenomenon being clearly governed by rhythmic law. This is illustrated by flowers with the following formula: $K4 C3 A4 + 3 G^4$. In this case it is

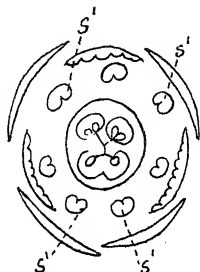


FIG. 82.—*Galanthus nivalis* (Snowdrop). Diagram of flower showing increase of members in alternate whorls, beginning with the calyx. s' , the four stamens of the outer whorl. (After Celakovsky.)

the first, third, and fifth whorl which has the increased number; in a *Crocus*-flower it was the second and fourth whorl which was so modified: $K3 C4 A3 G^4$. In some tulips examined there was an increase in all the whorls, but the first, third, and fifth had one more member than the rest: $K5 C4 A5 + 4 G^5$.

The present writer has seen, and Celakovsky has described, in many flowers of the snowdrop (*Galanthus nivalis*), the same rhythmic type of whorl-formation, according to the formula $K4 C3 A4 + 3 G^4$; in such cases the gynœceum may be imperfectly 4-merous (fig. 82).

This phenomenon of polyphyly tends to be accompanied in many flowers by a change in phyllotaxy from the whorled to the spiral type. An increase in

the number of members is apparently taking place from within outwards, as is natural, seeing that the apex was the primitive growing point of the shoot. The inauguration of the spiral arrangement is seen in the passage of a member of one whorl to the whorl next outside it; we see, for example, a member of the outer perianth (calyx) becoming transformed into a bract and displaced downwards, owing to the development of an internode; the gap so caused is filled by a member of the inner perianth-whorl (corolla), which in its turn is supplied from the andrœcium. This may be regarded as an instance of reversion (more or less imperfect) to a kind of spiral phyllotaxis. It causes a twisting of the peduncle of the flower. The change to the spiral arrangement is probably the primary factor in these flowers, and the formation of a bract from a sepal is a secondary phenomenon resulting therefrom.

Other instances will now be given of abnormal increase in the different whorls taken from various plants; in these cases the other whorls are, as a rule, unaffected.

(1) CALYX.

In the lesser celandine (*Ranunculus Ficaria*) the normal number of sepals is three; Celakovsky figures flowers with 4- and 5-merous calyx; as calyx and corolla are intimately united into one genetic spiral, the number of sepals will determine the position of the following petals. It is very frequent in many plants for an extra sepal to occur while no other part of the flower is modified.

A drawing of a flower of *Cypripedium insigne* showed the usually single posterior* sepal behind the lip divided into two, one on either side of the lip (Pl. XXXV); there is also a drawing by Mr. Hansen in the British Museum which shows the same thing in

* In all descriptions of Orchid-flowers the primitive condition of the flower is referred to before the ovary became twisted, except in those cases where these terms are between inverted commas.

C. Lawrenceianum; the present writer has seen the phenomenon in *C. insigne*, but in this case the two sepals were not quite free at the base.

Heinricher mentions that in a lady's slipper (*C. Calceolus*) these sepals were fused only at the base. It is also very interesting to note that Irmisch found that in the development of this species the two sepals are at first separate, and only at a later stage become united.

Heinricher states that in the Canadian *C. arietinum* they are normally quite free. This has been confirmed

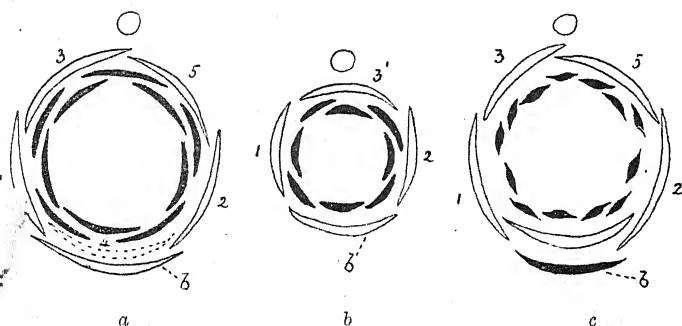


FIG. 83.—a, *Nymphaea alba* (White Water Lily). Quinesepalous flower. b, Normal flower of the same. c, *Nuphar luteum* (Yellow Water Lily). Normal flower for comparison with those of *Nymphaea*. b, bract. (Diagrams, after Celakovsky.)

from herbarium-specimens at Kew. These cases must be regarded as reversions to the primitive 3-merous condition of the calyx. The single posterior sepal has, of course, originally arisen by fusion of the two lateral ones which are always present in other orchids. A drawing by Mr. G. S. Saunders has also been seen showing complete fission of the anterior sepal.

In the white water-lily (*Nymphaea*) the calyx (including for the time being the transposed bract) consists of four orthogonally-arranged sepals (fig. 83 b), whereas in the yellow water-lily (*Nuphar*) there are five, of which sepals 3 and 5 are in the lateral posterior position (fig. 83 c). Celakovsky observed

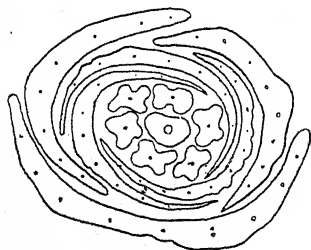
two very interesting and very rare abnormal flowers of *Nymphæa*: in one of these the median posterior sepal 3¹ of the normal flower was replaced by a two-fold sepal, in the other by two distinct sepals occupying precisely the position of sepals 3 and 5 in *Nuphar* (fig. 83 a); hence this represents without doubt the original structure of the calyx in *Nymphæa*. But this position of sepals 3 and 5 necessarily involves the former presence of a sepal (4) in the same (median anterior) position in which we find it in *Nuphar*. During the process of reduction from 5-mery to 4-mery in the calyx this median anterior sepal has disappeared owing to the transposition of the bract into that position. This reductive change has induced a similar change in the first two whorls of the corolla.

In *Veronica* frequently the odd posterior sepal, which has been eliminated owing to fusion of the two lateral posterior petals to form the single large median one (which would then come to lie opposite the median sepal, thus interfering with the law of alternation), becomes added to the diagonally-placed calyx. But there is a section of the genus named by De Candolle Pentasepalæ, in which a small fifth posterior sepal is normally present. Camus found a fifth posterior sepal occasionally present in *V. serpyllifolia*; but it also occurred sometimes in the anterior position, and opposite the small anterior petal, thus showing that its presence there was not due to torsion of the flower. It seems that Noll also observed in two flowers of *V. longifolia* an anterior fifth stamen; while Schlechtendal, in the same species, observed a 6-merous calyx having both a posterior and anterior median sepal. In all these cases the anterior sepal is probably due to bipartition of one of the lateral anterior sepals.

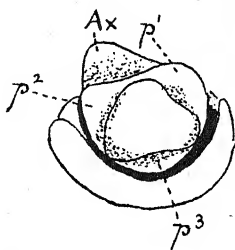
In most grasses, owing to the tendency of their flowers towards a 2-merous construction, whereby the two posterior sepals become fused to form a median posterior sepal and the two lodicules tend similarly to unite to form an anterior median petal, the anterior

median sepal necessarily tends to disappear in obedience to the law of alternation. Where, however, the original arrangement of the various floral members obtains, there is some likelihood of the reappearance of this third sepal, as was observed by Goebel in the development of the flower of a species of *Streptochæta* (fig. 85), the mature flower (fig. 84) showing no trace of it, and by Schacht in that of the flower of *Agropyrum giganteum* (*Triticum rigidum*).

An interesting case is described by Velenovsky in the male flower of *Salix aurita*, viz., the reappearance of the median anterior perianth-leaf. In the normal



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85

FIG. 84.—*Streptochæta*. Section of mature flower. (After Goebel.)

FIG. 85.—*Streptochæta*. Young flower showing presence of anterior sepal (p^3). p^1 , p^2 , posterior sepals. Ax , axis of spikelet. (After Goebel.)

flower of *S. pentandra* and some others this organ is also present in the form of a gland. But in the allied genus *Populus* this anterior perianth-leaf is normally present fused with the bracteoles to form the cupule-like structure. In the allied orders Juglandaceæ and Myricaceæ the two medianly-placed perianth-leaves are normally present as very small leaves. In two strongly virescent flowers of *S. aurita* the gland assumed a scale-like form.

Schmitz observed, in the abnormal cypress-spurges (*Euphorbia*) he examined, the appearance of one or two small leaves immediately below the anthers of the axillary "stamens," and also immediately below the

ovary of the female flower, and, in this case, situated above the circular swelling which always normally occurs below the ovary (Pl. XXXVII, figs. 1 and 2). Celakovsky states, probably correctly, that this swelling represents the former position of bracteoles, and corresponds to the articulation in the male flower. If so, then the small leaves above mentioned, in both male and female flowers, must represent the reappearance of sepals, which in *Euphorbia* normally are quite suppressed, but which in other genera are present as a normal character.

Normal examples of multiplication of the sepals are seen in the pappus of the Compositæ, and in the mangrove *Bruguiera* which has so many as twelve, although its near ally *Rhizophora* is possessed of the typical five.

It is very rare for an extra whorl of the calyx to occur which has arisen by *dédoublement* and not by metamorphosis of stamens or petals; such a case seems to be afforded by a toadflax (*Linaria vulgaris*) described by Roeper; the sepals of this extra calyx, being opposite the petals, had probably arisen from *dédoublement* of the rudiment of the petals.

(2) COROLLA.

In a flower of *Cypripedium Lawrenceanum* there were two lips (labella) alternating with the posterior sepal. This may perhaps be regarded as an attempt to restore the original alternation of parts which existed before the two lateral sepals became fused together behind the lip; here the converse has occurred: the petal has divided to form two. Plate XXXVI shows it in *C. Pitcherianum*.

In the annual larkspurs (*Delphinium Ajacis* and *D. consolida*) the single posterior spurred petal may be supplanted by two petals, which is clearly a reversion to the original condition, for this large single petal is the product of the fusion of two.

When, to form the inner transverse whorl of the

calyx of Cruciferae and Capparidaceae, the outermost corolla-whorl of the Papaveraceous type (from which the Cruciferae, etc., have been derived) became transformed into sepals, the four diagonally-placed petals in Cruciferae and Capparidaceae could only, as Celakovsky states, have been obtained by positive dédoublement of the two medianly-placed petals of the remaining (inner) whorl, and not by transformation of stamens. If this is so, then in the evolution of the Cruciferous flower we see an interesting admixture both of reduction and multiplication.

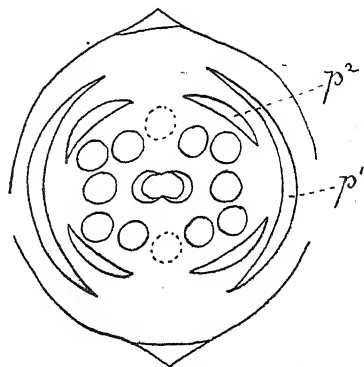


FIG. 86.—*Eschscholtzia*. Diagram of outer corolla-whorl of two (p^1), and inner corolla-whorl of four petals (p^2). (Cf. Cruciferae.) (After Benecke.)

Now, Benecke describes, as an abnormality, a precisely similar formation of four diagonally-placed petals by positive dédoublement of the two petals of the inner corolla-whorl (fig. 86). But this was in the Papaveraceous genus *Eschscholtzia*, in which, of course, there is also present an outer whorl of two transverse petals. So that here we have occurring in actuality the same phenomenon in the very order in which it was theoretically postulated by Celakovsky in order to account for the origin of the corolla of Cruciferae, etc.

In *Veronica* the large posterior median petal, the result of the fusion of two, reverts sometimes to the

original condition, and this is sometimes accompanied by the reappearance of the median posterior sepal in order to lie opposite the gap so formed.

The morphological importance of this division of the posterior petal is not affected, as Camus thinks it to be, by the fact, observed by him in four species, that the anterior petal divides still more frequently, for it is a not infrequent phenomenon in Dicotyledonous flowers for the number of petals to be increased by one or two members. Camus also saw 5-merous flowers due to bipartition of one of the lateral petals, 6-merous flowers due to *dédoublement* of both the anterior and posterior

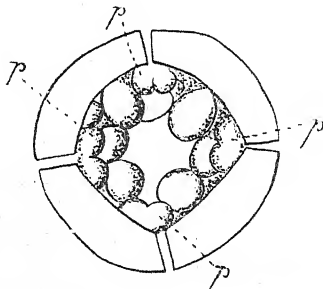


FIG. 87.—*Fuchsia*. Young flower-bud showing petal-rudiments (*p*) dividing collaterally. (After Goebel.)

petals, and, finally, 6- and 7-merous ones due to tripling of the anterior petal.

In the majority of grasses only the two anterior "lodicules" (representing, according to most botanists, vestigial petals) are present, the posterior one having disappeared owing to the fusion of the two posterior sepals into a single medianly-placed sepal. Schacht observed, in the development of *Agropyrum giganteum* (*Triticum rigidum*), in which the two posterior sepals were separated, the presence of the third posterior "lodicule." In two of the more ancient types of grasses, *Streptochaeta*, and some species of bamboo, three "lodicules" are normally present.

In "double" flowers the increased number of petals

is due to various causes ; one of these is by division of the petals at an early stage of their development ; if the division takes place collaterally there will be an increase

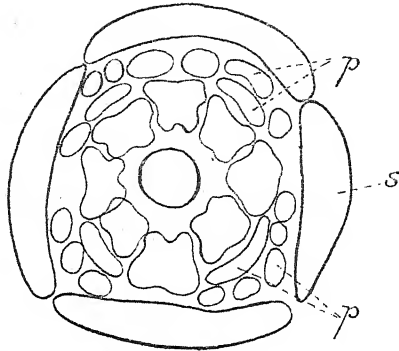


FIG. 88.—*Fuchsia*. Section of older flower showing serial and collateral division of petals. *s*, sepals ; *p*, petals. (After Goebel.)

in number of the members of the whorl ; if it occurs serially, *i. e.* in the antero-posterior plane, the number of whorls will be increased (figs. 87 and 88). Goebel

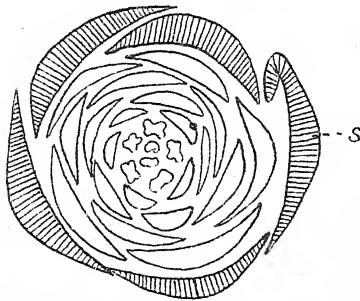


FIG. 89.—*Nerium Oleander*. Section of bud of flower showing pleiotaxy of corolla (= double flower). *s*, calyx. (After Goebel.)

gives a diagram of a flower of *Nerium Oleander* in which there were several whorls of petals, the rest of the flower being quite normal (fig. 89). The division may in some cases be congenital, and not at all perceptible during the development.

In many double roses a great increase in the corolla-whorls occurs, as also in double tulips. Goebel cites many cases, as in the blue lobelia (*Lobelia Erinus*), in which the earliest-formed whorls of petals were regularly 5-merous, but the later-formed ones irregular.

Lagerberg describes a flower of *Viola mirabilis* in which there was an extra inner whorl of three petals alternating with the normal ones, and bearing spurs: a case of partial pelory. Here we see the ternary character appearing in the corolla, which is a normal feature in the gynoecium.

Masters mentions a *Cyclamen* flower which had several extra whorls of petals; as there were no stamens, one of these whorls must probably be due to their petalody, the rest to dédoublement.

Interesting examples of the formation of extra whorls are afforded by a species of thorn-apple (*Datura fustuosa*). The simplest case is that in which there is an extra corolla, the rest of the flower being normal. In other cases, as cited by Goebel, the normal calyx and corolla were 5-merous; then followed a second corolla of about ten petals, being succeeded in its turn by a third and fourth corolla or even a greater number; the androecium and gynoecium were imperfectly formed. Goebel declares that this is not a case of dédoublement, as the extra whorls arise independently and alternate regularly; this statement, however, is made merely from the point of view of developmental data to which he attaches, as ever, an exaggerated importance. Knowing as we do that in other plants extra whorls of petals *do* arise by fission of the normal petals, it is highly probable that in *Datura* the extra whorls have arisen in the past in the same way, but now arise congenitally as quite distinct whorls, and, arising separately in this way, it has become possible for the members of the whorls to be rearranged so as to conform with the law of alternation. An intermediate stage, taking us one step nearer the ontogenetic origin of the phenomenon, is figured by Masters for the same

plant; here there are two extra corollas, but there is no alternation, the petals of all three corollas being opposite to one another. The middle corolla (the first extra one) is less developed than the innermost and is closely adherent throughout the greater part of its length with that,* separating into five petals at the top; its orientation is like that of the other two. N. E. Brown described (the present writer has seen the specimen) a very rare case of this phenomenon in the Asclepiad *Stapelia revoluta*; a single flower possessed two corolla-whorls, each with its annulus (so characteristic of the genus), the petals of the inner alternating with those of the outer whorl. Heinricher describes and figures flowers of the comfrey (*Symphytum officinale*) each petal of which bore on its outer (lower) surface, near the top of the corolla-tube, two small petaloid enations, and the remarkable point about them was that their orientation was normal and not reversed, as is the general rule with such enations; *i. e.* their upper surfaces are opposed to the lower surface of the corolla which bore them; they occurred with great regularity, but tended to disappear in the younger flowers of the inflorescence. The author regards them as stipules. Morren described a flower of "*Gloxinia*"† having a "catacorolla," composed of a tubular union of five petals not wholly resembling the normal ones in shape; the orientation of the "catacorolla" is the reverse of that of the normal one, the upper coloured surface being directed outwards. Its component petals are opposite those of the normal flower.

There is also a well-known form of this flower in which the corolla bears on its outer surface as enations five or fewer distinct petals having reversed orientation of their surfaces (fig. 90). This phenomenon has never yet been adequately explained. Morren considered the attached petals to be the rudiments of as

* Masters describes the same thing in a "*Gloxinia*" where the stamens had become changed into a gamopetalous corolla from the outer surface of which petaloid enations arose.

† *Sinningia speciosa*.

many flowers axillary to the calyx; but, as Goebel points out, these petals are not opposite the sepals. They are, as a matter of fact, opposite the petals of the normal corolla. Goebel includes this phenomenon amongst those of double flowers, but comes, like Masters, to the uninformative conclusion that they are merely "enations," which explains nothing. In abnormal flowers of *Primula sinensis* two or three similar

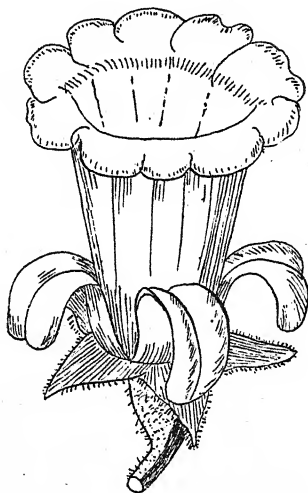


FIG. 90.—*Sinningia speciosa* ("Gloxinia"). Petaloid enations, with inversed orientation, on outer surface of corolla; also polymery of the corolla. (J. Weathers.)

enations were also seen on the outer surface of the corolla; their orientation was the same as in "*Gloxinia*."

The suggestion may be made that the "catacorolla" and the "enations" of "*Gloxinia*" are quite comparable with the first extra small corolla-whorl of *Datura* as seen in Masters' figure, which, we say, was also in the form of an enation from the innermost whorl, but, perhaps through being more corolla-like and better developed, exhibited normal orientation. The structures in "*Gloxinia*" are probably to be regarded as the representatives of an extra corolla-whorl, but

formed externally instead of, as in *Datura*, internally to the normal whorl; their position on the corolla may be merely a question of the mode of development of the single rudiment from which both have their common origin: if the rudiment divides at an early period into two equal parts, two equal corollas, exhibiting normal orientation, will result; if the innermost portion of the rudiment develops more strongly and ahead of the outer portion, the latter will appear, in the mature state, as an appendage of the former on its outer (dorsal) side, and this would give rise to such structures as we find in "*Gloxinia*" and in the abnormal corolla of *Datura fastuosa*; according to the degree of strength or weakness of the outer portion of the rudiment will be its appearance in the mature condition: a free independent corolla, a well-developed corolla-like enation on the normal one, or in the form of insignificant separate petaloid enations. Moreover, the more the corolla-character of the structure is maintained the more likely is its orientation to be normal; the more the enation-character predominates the more likely is the structure, like all enations, to obey the law of laminar inversion and exhibit inversed orientation of its surfaces (the two cases are exemplified respectively by the first extra whorl in *Datura* and the "catacorolla" of "*Gloxinia*").

The appearance of the enation-structure in certain forms of "*Gloxinia*" in the guise of separate petals, we can quite well understand, for it is well known that in many double flowers of the Gamopetalæ, as, for example, in the oleander, the corollas are polypetalous.

A similar phenomenon to that of *Datura* and "*Gloxinia*" is found occasionally in *Primula sinensis*, but here the enations are on the inner side of the corolla; which abnormality Masters classes amongst the double flowers. To quote his description: "In these flowers the calyx is normal, . . . the limb [of the corolla] is divided into ten fimbriated lobes.

About halfway up the tube, on the inner surface, are given off five supernumerary petals, opposite to as many lobes of the corolla. Some of the supplementary petals have a stamen in front of them, in the same relative position as in the normal flower. In some cases the back or outer surface of the supplementary petal is turned towards the inner or upper surface of the primary corolla, thus \frown ; while, in other instances, the front of the adventitious lobe is directed towards the corresponding surface of the original petal, thus \circ . Whether these supernumerary petals are formed by chorisism or by enation cannot, with certainty, be determined without examining the early stages of development." In this case we have the converse of that of *Gloxinia*, for here the outer lobes of the dividing petal-rudiments must have developed more strongly, and therefore ahead of, the inner, whereby the latter came to appear at maturity as mere branches or appendages of the former.

In *Datura*, "*Gloxinia*," *Primula*, and similar plants, the phenomenon described probably consists of an imperfect attempt on the part of the flower to form a second corolla* by the process of serial *dédoublément*, and this takes a varying form according to the idiosyncrasy of the flower or plant concerned. The phenomenon represents, therefore, a first step in doubling. From its consideration we see that there is not, as the older writers like Masters supposed, an essential distinction between "enation" and "chorisism," for both are but manifestations of one and the same phenomenon under different circumstances. Moreover, the statement that one organ is an "enation" from another is a purely descriptive one and sheds no light on the real nature of the phenomenon.

In *Siphium* and "*Gloxinia*" we see the two

* It may be, however, that in "*Gloxinia*" the "enations" may be the relic of an extra corolla; the present-day plants may be the descendants of a strain possessing two complete and independent corollas which was formerly in cultivation and has now become obsolete. This seems to have been Masters' view.

forms of dédoublement combined: the formation of an extra whorl of petals (imperfect, of course), and double the number of whorl-members caused by lateral fission (giving rise to polyphyly).

There is another possibility of explanation, and that is that the petaloid enations in *Primula* and similar instances are of the nature of the petaloid median loculi of the original anther from which the petal-blade sprang, which have become disjoined from the parent petal and appear as a basal ventral excrescence, or they may represent the basal upturned lobes of the anther, homologous with the corona of *Narcissus*.^{*} Where this excrescence is comparatively little developed, its orientation is, of course, the reverse of that of the petal; but in some cases it develops to the size of the parent petal itself, becoming individualized as a distinct, independent petal, so that the necessity for obeying the law of laminar inversion becomes abolished. If this is so, then this phenomenon in the petal is probably precisely the same as that described above in the foliage-leaf; in both cases all stages exist between small superficial enations and fully-developed, completely individualized foliar organs; and both would be homologous with the structure resulting from the ventral facial cohesion of two united basal lateral lobes with the midrib of the main leaf; thus the petaloid enations are also the homologues of the median laminæ in virescent, and of the median loculi in fertile anthers.

This view of the origin of the extra petals in *Primula* seems the more likely to be true inasmuch as there is a tendency for the petaloid stamens, as described by Masters in *P. vulgaris*, to develop enations which in some cases take the form of a median ovuliferous placenta probably corresponding to the median loculi of an anther. Masters also figures interesting transitional forms between small median enations, reminding one strongly of remnants of anther-lamellæ,

^{*} This can only be properly understood by reference to a later section where this subject is treated of.

and petaloid enations almost equalling the petals in size.* The tubular enations are comparable to the similar objects described by Celakovsky in *Narcissus*.

It is possible that this explanation may apply, not only to the *Primula*, but to all doubling where this is due to serial *dédoublement*, for it is obvious that each well-developed petal-like enation may itself repeat the phenomenon by which it arose, and so on, until a large number of such structures would be formed. Masters figures in his paper such a series of enations.

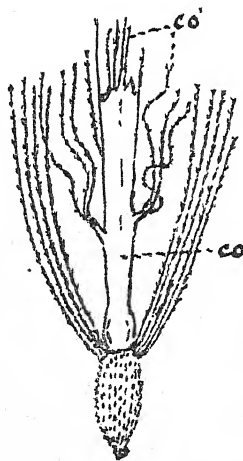


FIG. 91.—*Gnaphalium Leontopodium* (Edelweiss). Female flower showing extra outer corolla (*co'*) in form of a pappus. (After C. de Candolle.)

C. de Candolle observed a unique case in the edelweiss (*Leontopodium alpinum* β *nivale*); in some female and hermaphrodite florets there was an extra inner set of pappus-hairs united mostly in bundles, and attached along the sutures (*i. e.* alternating with the petals) of the corolla for varying heights, some adnate to its whole length (fig. 91); in the hermaphrodite florets the extra pappus-hairs had the character, not of the

* An explanation of the dorsal enations of *Primula*, etc., along the lines of extrorse anther-structure, is given elsewhere.

pappus-hairs in the normal hermaphrodite flowers, but of those of the female flower. That the extra pappus is not, as would naturally be at first supposed, the result of dédoublement of the normal pappus, but in all probability arises from dédoublement of the corolla, seems indicated by the fact that the observer noted in another floret supernumerary petals, free down to the middle of the corolla, and each terminating in a fringe of pappus-hairs. These represented, therefore, transitional forms between normal petals and pappus-hairs. Beauverd has seen a similar phenomenon to the above in *L. sinense* and *L. Evax* var. *fimbrilligerum*.

Another and striking method by which the number of petals is increased, and which may naturally be considered in this place, is that employed by those flowers whose axis becomes more or less elongated beyond the normal, the apex constantly adding new petals to the flower, as in the double cherry, in some flowers of which fresh petals are formed above the carpels; Goebel cites the formation of fresh petals above the petaloid carpels in *Lobelia Erinus*. A very extreme instance is afforded by those flowers which exhibit "petalomania," as in the abnormal madonna-lily (*Lilium candidum*) figured by Masters; here the floral axis is very greatly elongated so as to resemble a shoot; not only have all floral members become changed into perianth-leaves, but the apex of the axis has indefinitely added new petals to the whole; all these petals are, however, very much smaller and narrower than in the normal flower.

Collateral dédoublement may proceed in various ways: either the petal-rudiment may divide into two approximately equal parts, or it may cut off one or more smaller segments from itself, each of which becomes a complete petal, as has been observed in a stock (*Matthiola incana*) in which there were six petals: each of the extra small petals was still united laterally to its parent-petal at the base; this represented the first stage in doubling, to which this flower is very subject. Goebel

figures a flower of *Clarkia* in which division of the rudiment is rather late in appearing (similar in this respect probably to *Matthiola*), so that, instead of a number of separate equal petals being formed, the rudiment branches fore and aft into a number of subsidiary petals which in their turn branch or divide collaterally; so that the doubling in this flower is caused by the presence of a number of groups or bundles of petals.

This mode of "doubling" of the corolla by dédoublement, or by elongation of the axis and the independent formation of new petal-rudiments at the apex, must be held to be distinct from the "doubling" caused by petalody of the members of other whorls of the flower, a phenomenon to be considered in its proper place.

(3) ANDRŒCIUM.

Goebel found that in "double" flowers of *Petunia* there was a larger number of stamens present than the normal five, in one flower as many as twelve. In the flowers of this plant (Pl. XXXVII, fig. 3) as of some others, *e. g.* *Primula sinensis*, *Dianthus* (fig. 92), "doubling" is caused by division of the staminal rudiments and subsequent petalody of some or all of the products. In *Silene pendula* it was the rudiments of the inner whorl only which thus divided. This kind of division would, of course, be in the antero-posterior plane or serial, concerned as it is with the formation of fresh whorls.

In the genus *Primula* the five stamens are adnate to and opposite the petals, an arrangement which is anomalous, infringing the law of alternation, and which must somehow be explained. In the early stages it can be seen, as Duchartre and Pfeffer well showed, that the stamen-rudiment develops first and that of the petal somewhat later as a dorsal appendage thereof, a fact which led these authors to evade the difficulty above-mentioned by supposing that stamen and petal

together represented a single organ, and hence the flower possessed but three alternating whorls altogether. But here the usual mistake was made of relying on the misleading data of ontogeny. Eichler sets forth the correct view which, as always, is gained by the comparative study of forms. In other members of the Primulaceæ, e.g. the brook-weed (*Samolus*) and the yellow loose-strife (*Lysimachia vulgaris*), there occur, alternating with the stamens and petals, small scales, glands, or teeth which Braun regarded as a second corolla, but which are usually considered as pertaining to the andrœcium, and hence called staminodes. In the allied orders Myrsinaceæ and Sapotaceæ

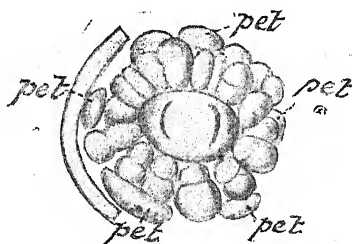


FIG. 92.—*Dianthus coronarius*. Serial dédoublement of stamen-rudiments to form a "double-flower." pet, normal petals. (After Goebel.)

these structures are often better developed, and bear either vestiges of anthers or are complete fertile stamens (as in *Isonandra*). Moreover, in a flower of the primrose (*P. vulgaris*) there was an outer whorl of stamens alternating with the petals and normal stamens. Hence we must assume that in the normal flower of Primulaceæ and Plumbagineæ the outer whorl of stamens has become completely suppressed and the inner whorl has congenitally fused with the corolla. In *P. Auricula* Marchand observed a third whorl within the normal whorl.

In the Iridaceæ it is the stamens of the inner whorl which have disappeared, so that the stamens which are present come to be opposite the carpels: an otherwise

illegitimate position. It is not at all infrequent in *Iris* for this inner whorl, in the form of stamens, staminodes, or petals, to reappear in abnormal flowers; in such cases it may be complete or incomplete. Heinricher, dealing with *Iris pallida*, has written excellent treatises on this subject. It is an interesting fact that in *Tritonia bracteata* the three stamens of the inner whorl are present in the form of staminodes.

No one can doubt that the flower of the lady's mantle (*Alchemilla*) has been reduced from a more richly-furnished type of flower such as occurs in most other members of the Rosaceæ. It has only four stamens, alternating with the four sepals. Hence we may regard it as a case of reversion when a flower, such as that mentioned by Eichler, produces an inner episepalous whorl of from one to three members.

In some of the Caryophyllaceæ three or four whorls of stamens, in place of the normal two, are sometimes found, probably also a case of reversion.

In the flowering rush (*Butomus umbellatus*) the six stamens are arranged in pairs opposite the sepals. Buchenau found in 10- to 11-androus flowers that the one or two extra stamens were inserted below the whorl of six, and exactly opposite the sepals. To explain their presence Eichler supposed that the original three rudiments split into three instead of two, and the middle of each three became pushed outwards; for if the extra stamens constituted a separate outer whorl, as Buchenau supposed, being opposite to the pairs of stamens of the normal whorl, they would violate the law of alternation. Celakovsky, as usual, saves the situation by finding that the presence of these extra stamens is a partial reversion to the ancestral condition in which two extra outer whorls were present; that these stamens belong to the outermost episepalous whorl, and that the epipetalous whorl is suppressed (Pl. XXXVII, fig. 4, and fig. 93 in text). For in the frogbit (*Hydrocharis*) these two outer whorls are actually present in the normal flower as staminodes. Thus, once

again the comparative method comes to the aid of those sufficiently enlightened to be aware of its value in solving such problems.

We next must consider certain abnormal orchid-flowers in this connection. As everyone is aware very great and far-reaching changes, in which abortion and excessive fusion and modification of various members of the whorls has played a marked rôle, have occurred during the evolution of the orchid-flower. As regards the arrangement of its parts the ancestral flower must have conformed to the Liliaceous type, with two 3-merous whorls in the perianth and andrœcium, and three carpels. The andrœcium is the whorl which has

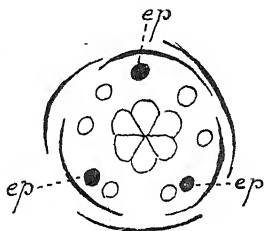


FIG. 93.—*Butomus umbellatus* (Flowering Rush). Diagram of flower shown in Plate XXXVII, fig. 4. (After Celakovsky.)

undergone most change. Of the outer whorl only one fertile stamen remains, viz., the anterior one which appears in the column; the two lateral posterior ones are only represented by ridges at the sides of the lip with which they have become intimately fused. All three stamens of the inner whorl are suppressed, having apparently become wholly incorporated into the column whose wing-like appendages perhaps represent traces of them.

In *Cypripedium*, however, the anterior lateral stamens of the inner whorl are present and fertile, while, in other genera, the fertile stamen of the outer whorl is present, though sterile and in the form of a large staminode.

In some orchids, however, there are normally a

larger number of stamens present. *Arundina pentandra* has all three of the outer whorl and the two anterior lateral ones of the inner whorl present and fertile. *Epidendrum Ottonis* is triandrous, A_1 of the outer whorl, and a_1 and a_2 of the inner whorl being present. In *Neuwiedia* (of the sub-order Diandræ) the staminode of *Cypripedium* is present in the form of a fertile stamen.

We should naturally expect cases of reversion, under one form or another, to occur in abnormal flowers; and such are quite frequent. In Masters' works will be found a fairly full account of them.

In a flower of *Pogonia ophioglossoides*, described by Asa Gray, the perianth was normal. There were two accessory labella just in the position of the two suppressed stamens of the outer whorl (A_2 and A_3), and there was a small petaloid structure corresponding to A_1 . In another flower the two lateral stamens of the inner whorl (a_1 and a_2) were represented in the form of slender filaments. The third stamen of the inner whorl and the stigmas may be represented by some or all of the remaining petaloid structures.

Flowers of *Cattleya labiata* and *Odontoglossum crispum* were seen with three stamens in the column. The two extra ones probably represented stamens a^2 and a^3 of the inner whorl, but this was not certain. The rest of the flower in each plant was normal.

Schlechter and Fischer describe flowers of *Odontoglossum grande* which were most perfectly peloric throughout. All three petals were alike and mainly resembled the normal lateral petals; the column consisted of three anthers, all exactly alike, and, therefore, presumably all belonging to the outer whorl; there were three rostellæ and stigmas (Pl. XXXVII, figs. 5 and 6).

Masters saw a flower of *Cypripedium barbatum* in which the staminode (A_1) of the outer whorl was fertile. In another flower the converse condition to that normally obtaining occurred, viz., the staminode

A_1 was fertile, while the two normally fertile stamens of the inner whorl (a^1 and a^2) were staminodial. In a flower of *C. Spicerianum* all the three stamens of the inner whorl (a_1 , a_2 and a_3) were present and fertile. He also observed a tetrandrous flower of *C. Lawrenceanum* which was composed as follows: A_1 (the usual staminode), a_1 , a_2 fertile, and a_3 developed as a lip which lay within the normal lip. Hexandrous flowers occurred in a *C. Sedeni*, all six stamens being present; A_1 and a_3 were fertile, while all the rest were in the form of saccate lips (fig. 94).

Rolfe mentions a flower of *Cattleya labiata* which had

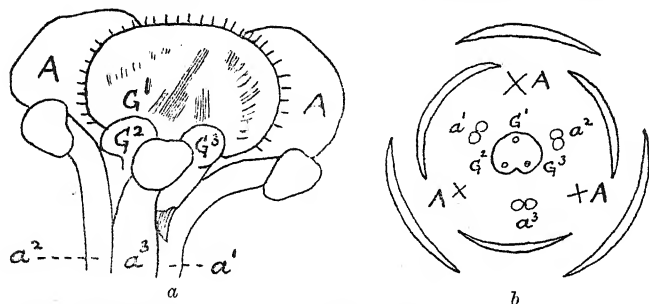


FIG. 94.—*Cyripedium Sedeni*. a, Column showing presence of stamen a^3 of the inner whorl. b, Diagram of the same flower. (After Masters.)

three fertile stamens, but the lip was developed as an ordinary petal; thus the flower reverts to regularity. It is very rare for the posterior stamen of the inner whorl (a_3) to be developed, but an example is afforded by *Uropedium* (merely a peloriate form of *Pachypedium caudatum*); therefore in this all three stamens of the inner whorl are fertile. Another instance has just been cited in *C. Sedeni*.

The interest of the above facts lies in the reversion, for the most part partial, which they exhibit to the ancestral structure.

Positive dédoublement in the above instances takes the form of the reappearance of vanished members.

In abnormal flowers of the *polyanthus narcissus*

(*N. Tazetta*) Celakovsky observed one to two extra whorls of stamens, of which the innermost was for the most part reduced to sterile filaments.

In the Zingiberaceæ the anterior of the three staminodes constituting the outer whorl of the andrœcium is normally absent. This is owing to the fact that the labellum, belonging to the inner whorl, is in the same median plane, and would therefore be immediately opposed to this staminode; as the law of alternation will not admit of this, the staminode inevitably becomes suppressed. Both Eichler and F. Müller observed, in some abnormal flowers of *Alpinia*, the reappearance of this anterior staminode. What

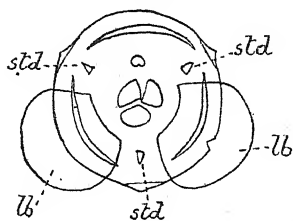


FIG. 95.—*Alpinia*. Reappearance of anterior stamen (staminode) (*std*) of outer whorl; division of anterior labellum (*lb*) of inner whorl. (Diagram, after F. Müller.)

was the direct cause of this? A very illustrative one, viz., the division of the median labellum (representing a fusion of the two anterior lateral stamens of the inner whorl) into its original constituents, which then assumed their normal lateral position (fig. 95). The law of alternation then permitted of the formation of the third anterior staminode.

In peloric flowers of Scrophulariaceæ, such as occur in *Scrophularia*, *Pedicularis*, etc., the fifth (posterior) stamen, normally either absent or in the form of a staminode, is usually as fully developed as the remaining four. In the flowers of the mullein (*Verbascum*), which are almost actinomorphic, there are normally five fully-developed stamens present.

The genus *Veronica* of this order possesses only two

stamens, viz., the two posterior lateral ones, most of the other genera having at least four stamens. Flowers of *Veronica* occur abnormally with three, four, or five stamens: an interesting case of reversion.

The majority of the Oleaceæ have only two stamens, which may be either the two lateral, as in the lilac (*Syringa*), or the two median ones (*Jasminum*), of the ancestral tetrandrous flower; this last is to-day represented by *Tessarandra*, which has four stamens. Buchenau observed a flower of *Syringa* in which the two lateral stamens were replaced by two small petals, and the two median stamens of the ancestor had reappeared; this latter phenomenon being probably the cause of the former, or *vice-versâ*.

In most species of willow (*Salix*) the number of stamens is two; many observers have noted the presence in abnormal flowers of three, four, or five stamens; clearly a reversion to a condition which is the normal feature in other species, such as *S. triandra* and *S. pentandra*, which represent, in their androecium, older types than the more common diandrous form. The poplar (*Populus*) must be regarded as a still older type in which polyandry obtains.

The normal flower of Cruciferæ has an outer whorl of two lateral stamens and an inner whorl of four, approximated in pairs in the median plane. According to the law of reduction, which we are now coming to perceive is of very wide-spread prevalence in the vegetable kingdom, the Cruciferous flower is really a much later reduced condition of that of the closely-allied order Capparidaceæ, in typical forms of which the flower is polyandrous. Celakovsky has elaborated the whole matter admirably, and the reader is referred to his treatise on this and other orders for what is probably the best and most thorough-going account of floral evolution. Abnormal flowers of the wall-flower (*Cheiranthus Cheiri*) have been seen with eight stamens, four in the outer whorl instead of the usual two (fig. 96 a). This is, on the theory of reduction, a

reversion to the immediately preceding ancestral condition in which the outer whorl consisted of two median and two lateral stamens. This condition has in its turn been derived from an earlier one in which the outer whorl of stamens consisted of eight members, placed at equal distances apart, while the inner whorl possessed four diagonally-placed members. This theoretical construction of the ancestral Cruciferous flower drawn up by Celakovsky receives complete and full substantiation from the structure of some abnormal flowers of *Cleome spinosa* which he has placed on record. This genus belongs to the Capparidaceæ. Normally this species of *Cleome* has the floral con-

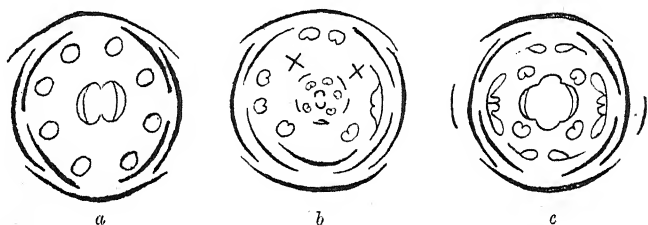


FIG. 96.—a, *Cheiranthus Cheiri* (Wallflower). Outer whorl of androecium of four stamens. b, *Cleome spinosa*. (After Eichler.) c, The same. (After Celakovsky.) Diagrams.

struction typical of Cruciferæ (unlike others with a pleiandrous androecium).

In one of the abnormal flowers the two lateral stamens of the outer whorl had become petaloid, although still bearing anthers. In the median position, and also in the outer whorl, were four stamens, all in the form of staminodes, each bearing only half an anther, and approximated in pairs. In the inner whorl were four diagonally-placed fertile stamens. In the centre of all was a pistil of four carpels, the two median ones being much smaller than the normal lateral ones (fig. 96c). If this structure of the abnormal flower, so different from that of the normal one, represents a progressive phenomenon, it can, says Celakovsky, have no bearing or explanation whatsoever on the structure

of the normal flower. What prove it, on the other hand, to be a retrogressive, ancestral structure, are firstly, the petaloid and staminodial forms under which the stamens of the outer whorl appear, and secondly, the weak, imperfect (as regards size) development of the median carpels. For this is just the way in which vestigial organs do tend to reappear or to be formed before they finally die out. In another flower one of the stamens of the outer whorl was petaloid and anther-bearing, the other was represented by two fertile ones (showing a further step backwards towards the ancestral condition); of the four stamens of the inner whorl the two posterior ones had completely vanished. In the centre were five carpels; beyond these slight proliferation had occurred, as the whorls were further added to by five stamens and two carpels (fig. 96*b*).

Such cases as those just mentioned represent transitions (the normal flower of *Cleome spinosa* itself forming a link between Cruciferae and Capparidaceae) between that prevailing in the normal flower of the majority of Cruciferae and that of the normal flower of the less frequent genera *Megacarpaea* and *Holargidium* in which the flowers may be 10- or 16-androus,* and which thus approximate to, and form links with, the typical Capparidaceae.†

Hermaphroditism.

Female flowers may become once more bisexual by the reappearance of the stamens which had become totally suppressed in the original hermaphrodite flower.

In *Begonia* hermaphrodite flowers were observed due to the production of a group of stamens on one side of the female flower between the two broad petals;

* Velenovsky observed flowers of the wallflower in which the two stamens of the outer whorl were each represented by a group of three stamens: an outermost and two inner ones.

† Velenovsky, while allowing that the ancestors of the Rhœadales had a polymeric androecium, regards this condition in Cruciferae as a recently-acquired phenomenon. Celakovsky's view of the matter is, however, here supported.

this was accompanied by degeneration of the inferior ovary, the number of carpels becoming reduced (fig. 97). Female flowers of the hornbeam (*Carpinus Betulus*), better developed than normally, each contained a single stamen. Female flowers of the red campion (*Lychnis dioica*) infested by the mycelium of *Ustilago violacea* become hermaphrodite owing to the development of the otherwise rudimentary stamens.

Robbins found that the peloric ray-florets of *Gaillardia aristata*, which in their normal zygomorphic condition are sterile (neuter), were furnished with

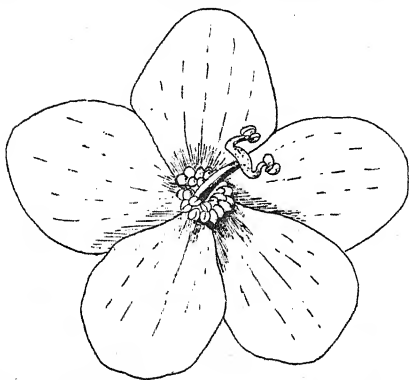


FIG. 97.—*Begonia*. Female flower become hermaphrodite through the appearance of stamens. (J. Weathers.)

stamens and pistil, both perfectly developed. This is one of the very numerous instances in which one reversionary change is concomitant with another with which it would seem to be closely correlated.

The ray-florets of the Compositæ represent differentiations of the disk-florets in two main directions: zygomorphism of the corolla and unisexuality or sterility.

Blaringhem obtained by artificial mutilation hermaphrodite flowers in the maize; but the stamens were never fertile, and they did not appear until a little before maturity of the plant, long after the ovaries had been fertilized. This is a good case of the late appear-

ance of ancestral characters. These hermaphrodite flowers differed completely from those sometimes observed on the male panicle.

C. G. Fraser describes an interesting case of traumatic reversion in *Acer Negundo*. A branch of a female specimen of this dioecious species had become almost severed from the trunk; as a direct consequence, it would seem, of this wounding, the flowers borne by this branch developed stamens as well as carpels. A remarkable fact was that the characters of the inflorescence and calyx, and the number of the stamens, were intermediate between those of the normal male and female flowers of the species.

In all these cases an increase of floral members is brought about by the reappearance of some which were formerly present, but had become suppressed.

(4) GYNŒCEUM.

a. CARPELS.—Reference has already been made to those tulip-flowers which showed an outer whorl of six, and an inner of three carpels; in those cases where six carpels are present it is probable that they would have been in two whorls if the vertical space on the floral axis had allowed of it.

Miss Gibbs describes the presence of a second whorl of carpels as occurring above the normal one in *Cerastium quaternellum*. Prain observed the same phenomenon in the rice.

The character of the navel orange is derived from the fact that an imperfect second whorl of carpels arises above the normal whorl; sometimes a completely-formed second small orange is so developed at the top (fig. 98) or in the inside (fig. 99) of the normal one. These facts show the presence of a floral axis in the centre of the fruit.

A similar phenomenon occurs occasionally in the tomato; and Masters gives instances of it in other plants as well.

In the larkspur (*Delphinium*), especially in double flowers, a larger number of carpels than the normal

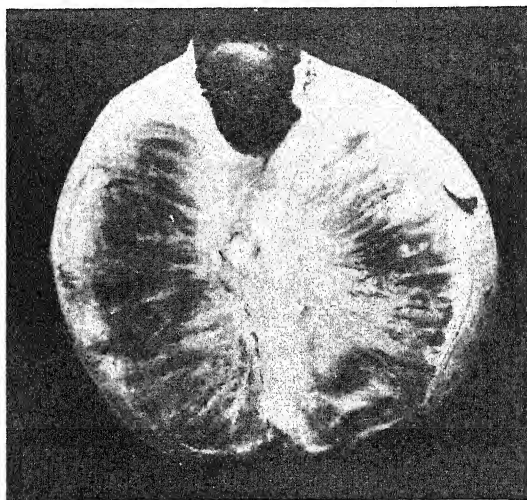


FIG. 98.—*Citrus Aurantium* (Orange). Secondary orange (whorl of carpels) formed at apex of primary one (as seen in longitudinal section of the latter).

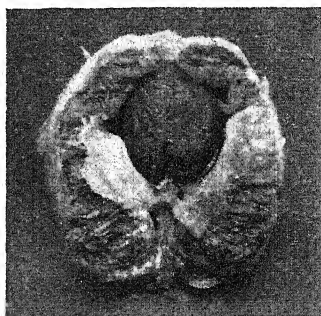


FIG. 99.—*Citrus Aurantium* (Orange). Secondary orange (whorl of carpels) formed within the primary one (as seen in longitudinal section of the latter).

may be laid down in spiral succession on the more elongated axis of the flower.

In *Cephalotaxus* there was observed, on the slightly elongated floral axis, which usually in its normal state produces a single pair of ovules only, an extra pair formed above; but one of these is usually in the form

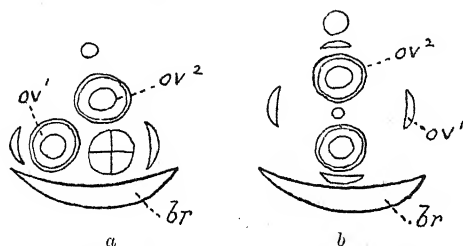


FIG. 100.—*Cephalotaxus drupacea*. *a*, The second whorl consists of one ovule only. *b*, Flower with second whorl of ovules (*ov*²) alternating with the first whorl of metamorphosed ovules (*ov*¹). *br*, bract. Diagrams.

of a small foliar organ; sometimes, when the two normally-situated ovules are replaced by similar foliar organs, the ovule occurring in the second whorl is the only one in the flower (fig. 100). Celakovsky is doubt-

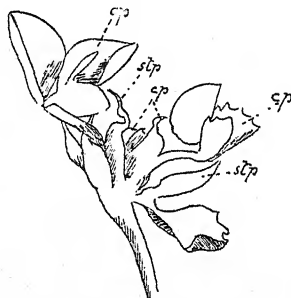


FIG. 101.—*Trifolium repens* (Dutch Clover). Flower with two or more extra carpels (*cp*). *stp*, stipules.

less correct in regarding, on comparative grounds, the Taxaceous ovule as representing a carpel reduced to one of its ovules; so that in these abnormal flowers there are two whorls of carpels represented.

In those plants which have normally a reduced

number of carpels as compared with that of members of the other whorls of the flower, it is quite common to find what we may regard with almost complete certainty as a reversion to a larger number, sometimes to that typical of the other whorls.

A flower of the toadflax (*Linaria vulgaris*) had five carpels instead of the two characteristic of the order Scrophulariaceæ; in this case the original number five, of which all whorls of the flower once were composed, has been restored.

In the Leguminosæ there has been very great reduction in the gynœceum, which has been left with only a single carpel. Reversions, partial or complete, would be expected to occur from time to time. *Mimosa* has occasionally produced five carpels: a case of complete reversion to the number of members possessed by the other whorls. Flowers of *Trifolium repens* were seen with two and three carpels respectively (fig. 101), and those of the scarlet runner (*Phaseolus multiflorus*) with two (fig. 102); in this last case the extra carpel is not always so well developed as the others, sometimes being almost vestigial; as Drabble and others describe, the two carpels, which are placed in the antero-posterior plane, are sometimes fused by their ventral

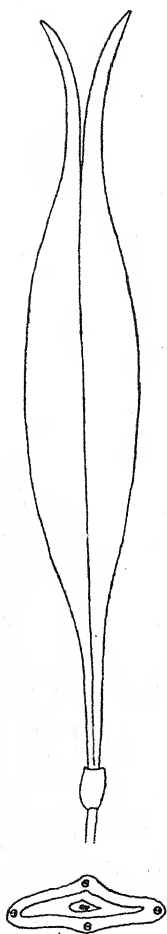


FIG. 102.—*Phaseolus multiflorus* (Scarlet Runner) Bicarpellary fruit forming a syncarpous ovary, with section.

sutures so as to form a bilocular ovary, at other times by their margins to form a unilocular ovary.

In the section *Pruneæ* of the *Rosaceæ* there is normally but a single carpel; this is one of the most extreme cases of reduction that we know of, for the stamens are indefinite in number, and in other sections of the order the carpels are also indefinite. In double flowers of the cherry two carpels are almost invariably present (Pl. XXXVIII, fig. 1), and in this genus (*Prunus*) and *Amygdalus* so many as five are sometimes found.

In *Spilanthes*, one of the *Compositæ*, in which order two carpels are the rule, there have been observed indications of so many as five carpels.

It was mentioned on a previous page that the flower from which the modern Cruciferous bloom has been directly derived may be regarded as one having two whorls of stamens of four members each; in that ancestral-flower there must also have been a whorl of four carpels present, for in certain abnormal cases four carpels, or indications of the missing two median ones, are found. There is a permanent "sport" of the marsh yellow-cress (*Nasturtium palustre*), placed by some authors in a separate genus and termed *Tetrapoma barbareæfolia*, which usually possesses four carpels all equally developed. This must be regarded as a reversion to the older condition. This plant, however, sometimes produces 2- and 3-carpellary fruits. *Nasturtium globosum* and *N. amphibium* also have been found with 3-carpellary fruits. *Holargidium* normally possesses four carpels.

Cleome spinosa, of the *Capparidaceæ*, normally has two carpels, like the *Cruciferae*. Abnormal flowers (see p. 86, fig. 96 c) have four carpels, two extra smaller ones being present in the median plane. This plant obviously constitutes an interesting link between the two orders.

The sycamore (*Acer Pseudoplatanus*) sometimes has extra winged carpels present (Pl. XXXVIII, fig. 3). Turpin figures a heath with one or two extra whorls of carpels present (fig. 103).

In grasses, regarded as a whole, very great reduction in the pistil has occurred; however, in *Ochlandra* there are many carpels; in *Streptochæta* and *Bambusa* there are three, *i. e.* equal in number to the components of the remaining whorls. In most grasses there is a single carpel, but with two stigmas. Celakovsky has shown that this is a case of incomplete reduction from two carpels to one, comparable to a double leaf. Occasionally a reversion to the original three carpels occurs in the flower, as in the case of *Schœnodoros elatior* mentioned by Nees. There are, however,

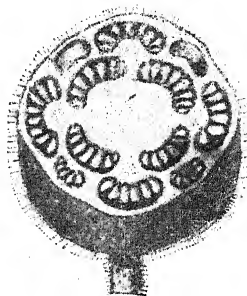


FIG. 103.—*Erica Tetralix* (Cross-leaved Heath). Transverse section of fruit, showing one or two extra whorls of carpels. (After Turpin.)

several cases in which three stigmas make their appearance; a proof that the immediate ancestors had three carpels.

Schlechter and Fischer described a peloric flower of the orchid *Odontoglossum grande* in which the gynoecium was perfect, there being three rostellæ and three stigmas on the interior side of the column, whereas in the normal flower of orchids there is only one rostellum present, and at most two stigmas. No more perfect peloric orchid-flower than this has ever been described (see Plate XXXVII, fig. 5).

A crocus-flower, exhibiting rhythmic alternation in the numerical constitution of its whorls, had four carpels (fig. 104).

In the filbert or hazel (*Corylus Avellana*) three carpels are developed in the flower. Normally, however, as the fruit matures, two of these become abortive, so that the ordinary nut consists of a single carpel. Now and again a nut appears which is con-

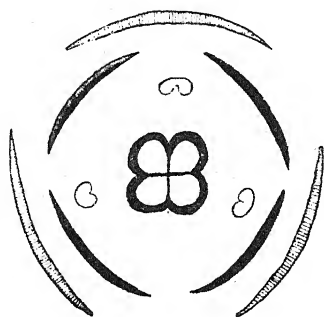


FIG. 104.—*Crocus* sp. Diagram of flower with the formula
K3 C4 A3 (+ 0) G₄.

siderably larger than usual and whose trilobed contour shows it to be composed of the original three carpels of the flower all equally or sub-equally developed (fig. 105).

The adhering disks of the tendril of the grape-vine

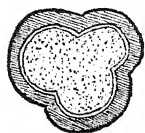


FIG. 105.—*Corylus Avellana* (Hazel). Fruit with three almost equally-developed carpels. Transverse section.

(*Vitis*) are probably the modified swollen tips of the pedicels of the inflorescence; occasionally they revert to the original condition and produce a grape. This is one of the facts which prove the vine-tendril to be a modified inflorescence. It must therefore be due to the reappearance of floral members (carpels) which have been completely suppressed (Pl. XXXVIII, fig. 4).

In the maidenhair tree (*Ginkgo biloba*) we find abnormally an increase of the number of carpels (here reduced to ovules), which also become long-stalked; doubtless a case of reversion, the normal female flower of *Ginkgo* being palpably a reduced structure (fig. 106).

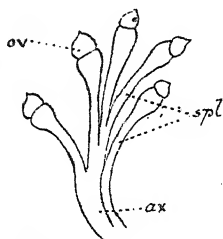


FIG. 106.—*Ginkgo biloba* (Maidenhair Tree). Female "flower" with five stalked ovules (= carpels). (After Seward & Gowan.) *ov*, ovules; *spl*, carpels; *ax*, axis of flower.

Hermaphroditism.

Many flowers of monœcious and dicœcious plants have become purely male owing to the complete suppression of the pistil; such flowers frequently revert to the original bisexual condition by forming once

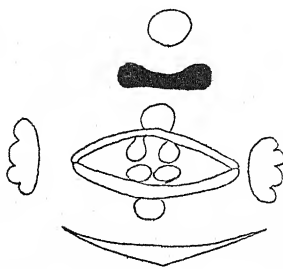


FIG. 107.—*Salix aurita*. Diagram of hermaphrodite flower shown in Plate XXXVII, fig. 5. (After Velenovsky.)

more a pistil in their centre. Such occur sometimes in the male inflorescence of the maize. The same phenomenon may be found in willows, *e.g.* the goat willow (*Salix caprea*) and *S. aurita* (Pl. XXXVIII, fig. 5, and fig. 107 in text); in *S. caprea* Heinricher

found flowers with the usual pair of transversely-placed stamens and a pistil between them.

Giard describes male flowers of the sedge (*Carex præcox*) becoming hermaphrodite owing to infection by the fungus *Ustilago caricis*, those of the grass *Buchloë dactyloides* infected with *Tilletia buchloëana*, and *Andropogon provincialis* with *Ustilago andropogonis*.

Leake describes the reappearance of carpels in the male flower of the date-palm (*Phoenix dactylifera*) (fig. 108).

Robbins found that the peloric ray-florets of *Gaillardia aristata*, which in their normal zygomorphic

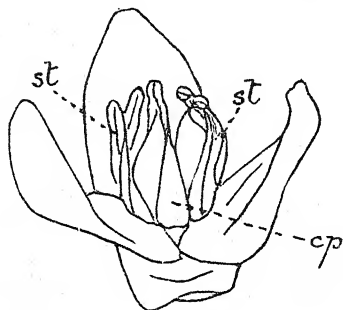


FIG. 108.—*Phoenix dactylifera* (Date-palm). Hermaphrodite flower due to the reappearance of carpels (*cp*) in the male flower. *st*, stamens. (After H. M. Leake.)

condition are neuter, produced both stamens and pistil in perfect development.

b. OVULES.—The ovules, here regarded as lateral segments or appendages of the carpel, may be increased in number. One or two instances of this may be given. Masters describes a carpel of *Ranunculus Ficaria* which, in place of the normal single one, bore two ovules, placed not, as usually is the case, on the carpellary margins, but on the surface of the carpel some little way from the edge. Small mentions an ovary of the groundsel (*Senecio vulgaris*) containing two laterally-situated ovules. Masters figures a leafy carpel of the "green rose" bearing two ovules, one on each

margin (Pl. XXXVIII, fig. 6). Payer has shown that in the development of the normal carpel two ovules arise, of which one becomes abortive later; hence teratological and developmental evidence combine to show what the ancestral condition was like.

In the same way, in a species of *Zamia*, three ovules were seen instead of the normal two.

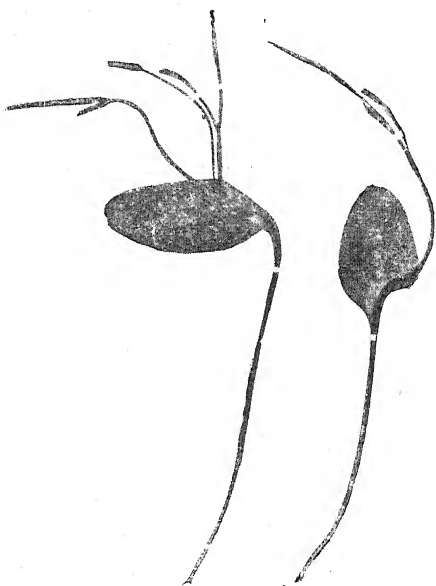


FIG. 109.—*Ophioglossum vulgatum* (Adder's-tongue Fern). Bifurcating "spikes" and tendency to increase in their number. (After Freiberg.)

(5) SPOROPHYLLS OF CRYPTOGRAMS.

a. SPOROPHYLL-SEGMENTS.—In the adder's-tongue fern (*Ophioglossum vulgatum*) and the moonwort (*Botrychium*) the sterile portion of the sporophyll may fork more or less deeply; forking, to the second or third degree, is the normal condition in *O. palmatum*; the sterile is merely the terminal portion of the entire sporophyll. It occasionally also happens in *O. vulgatum*

that two fertile "spikes" occur in close proximity on the upper surface of the frond, instead of the usual single one; or the normal "spike" may be divided into three or four branches (fig. 109). In *O. palmatum* there normally occur many "spikes," and, for the most part, on the upper surface, but quite close to the margin (Pl. XXXVIII, fig. 7); in some cases a "spike" is actually marginal. Roeper and Goebel are, doubtless, correct in stating that the fertile



FIG. 110.—*a*, *Aneimia*. Frond showing the pair of approximated basal fertile pinnae. *b*, *Botrychium obliquum*. Frond showing two fertile "spikes" partly united by their stalks. (After Chrysler.)

"spikes" of the Ophioglossaceae represent lateral pinnae of the frond which have become displaced on to the ventral surface. The basal fertile pinnae of the Schizaeaceous fern *Aneimia* offer a perfect analogy in support of this view; these pinnae converge across the face of the frond, turning their dorsal surfaces towards the axis (fig. 110 *a*). We can imagine it easy for them to fuse by their outer margins and to come in the course of time to be seated, as a single "spike," on the upper surface of the frond. This was Roeper's view of the origin of the Ophioglossaceous fertile "spike." It is a very plausible one. The abnormal branching

of the "spike" in *Ophioglossum* may be regarded as supporting this view. The "spike" is attempting to revert to the original condition of two lateral "spikes."

Chryslar, in an excellent paper, proves, once and for all, both by conclusive anatomical evidence and by teratological data, that the fertile spike in *Ophioglossum* and *Botrychium* represents a fusion-product of two lateral segments of the sporophyll, one from either side, and in *Helminthostachys* the anatomy shows that it represents a single lateral segment. In an abnormal specimen of *Botrychium obliquum* he observed two fertile "spikes" partly fused together by their stalks (fig. 110 b), and below them a larger fertile "spike" representing the complete fusion of two.

The fertile "spikes" of *O. palmatum* are for all practical purposes marginal; some are actually so; but the strong distinction which Bower makes between marginal and submarginal appendages is beside the mark. Ovules, universally regarded as marginal appendages of the carpel, are very frequently, either in their normal or virescent form, seated on the surface of the carpel, some little distance from the margin, as in the case of *Ranunculus Ficaria* cited above. Marginal structures become very easily displaced on to the surface of the leaf, a fact which does not prevent their being regarded as morphologically marginal out-growths.

Regarded in this light the Ophioglossaceæ fall naturally into line in the fern-series as regards the conformation of their sporophylls.

The wider homologies of these fertile segments of the sporophyll in Ophioglossaceæ may here be alluded to; they may be described as "enations" from the upper surface of the leaf, and, as we have seen, they represent the fusion by the outer margins across the ventral surface of the sporophyll of two of its basal lateral lobes; the single lobe so formed is also for a certain distance united by its ventral surface to the median portion of the main leaf; hence we have

here once more a structure which is the homologue (to cite one instance) of the petal-enations of *Narcissus*. In that plant, as showing that the ventral excrescence or corona really represents the fusion of two lateral lobes of the perianth-leaf, Celakovsky observed and figured perfectly petaloid stamens provided with a lateral lobe on each side which had the exact consistence, colour, and form of the corona. Now, just as the petaloid enations of *Narcissus* may equal in development the leaf which bears them, in the same way do the fertile "spikes" of *Botrychium* and *Helminthostachys* equal in size and elaboration the sterile portion of the

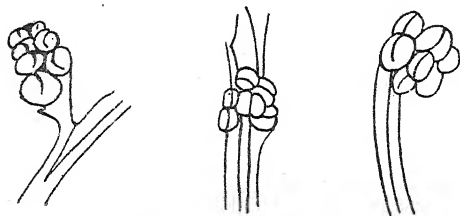


FIG. 111.—*Psilotum triquetrum*. Plurisporangiate sporophylls.
(After M. G. Sykes.)

frond which bears them. (Conversely, the sterile lamina, as seen by Hergt in *Ophioglossum vulgatum*, may be abnormally lobed, after the manner of that of *Botrychium*; probably a reversion.)

In the Psilotaceæ the sporophylls, normally excessively reduced in their conformation, may abnormally become rather more complex. A. P. W. Thomas describes most interesting cases in *Tmesipteris*; the normal sporophyll is forked, and bears at the point of forking a single synangium. The abnormal ones are, however, repeatedly forked, and the synangia correspondingly increased in number. In other cases the synangium is raised up on a distinct stalk of its own. He also mentions, and Miss Sykes describes in detail, abnormal sporophylls of *Psilotum* which are repeatedly bifurcated in a similar way, with a great corresponding

increase of synangia (fig. 111). These cases are almost certainly reversions, as Thomas suggests, to the more complex type of sporophyll met with in the ancient Sphenophyllales; for in both *Cheirostrobis* and *Sphenophyllum* (certain species) the sporophyll is repeatedly forked, and moreover the sporangia are borne on special stalks or sporangiophores. It is now generally admitted that the nearest modern relatives of the Sphenophyllales are to be seen in the Psilotaceæ. We have here, therefore, another excellent instance of the light which may be thrown by abnormalities on the ancestry and morphological nature of highly modified, and on that account, obscure and inexplicable structures.

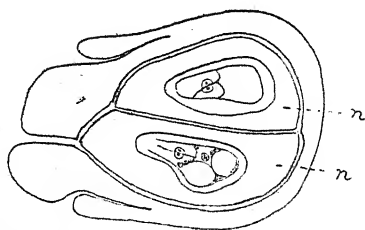


FIG. 112.—*Cerastium glomeratum* (Mouse-ear Chickweed). Two nucelli (megasporeangia) in one ovule (longitudinal section). (After Miss Gibbs.)

b. SPORANGIA.—In *Ginkgo* it is not uncommon to find stamens bearing three or four, instead of the usual two, pollen-sacs. Undoubtedly a reversion to the condition in the ancestry where the sporophyll was much better developed and on a larger scale.

The presence of two nucelli (megasporeangia) in an ovule is of not very infrequent occurrence. Hofmeister cites it as occurring in *Morus alba*, Misses Benson and Sanday in *Carpinus Betulus*, and Miss L. S. Gibbs in *Cerastium* (fig. 112).

Bower observed a very rare case in *Lycopodium rigidum*, in which two sporangia were present on the sporophyll instead of the usual single one (Pl. XXXVIII, fig. 2).

GENERAL CONCLUSIONS.—More will be stated under this heading in a later section, when reduction-phenomena are considered. In the meanwhile it may be said that the phenomena of positive dédoublement are in a general way reversional in character. Some of them, however, may be regarded as exhibiting reversion in one aspect, but not in another. For instance, in the lily afflicted with "petalomania" the elongation of the axis may be regarded as a reversion, as also the formation of great numbers of spirally-arranged foliar organs; but the petaloid character of the latter cannot be so regarded. Many of the cases of dédoublement may perhaps be considered as early stages in fasciation of the flower. Whether a reversionary meaning is to be attached to the formation of extra corolla-whorls in *Datura* and *Sinningia* it is difficult to say. If so, it can only be in the wider, vaguer sense of the term.

"Positive dédoublement" is merely a (frequently reversionary) increase in the number of whorls or members of whorls. "Fasciation" is an increase in the number of whorl members representing early stages in the splitting of the flower into two or more.

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5. DIALYSIS.

This term has been usually applied to the dissociation of members belonging to the same floral whorl which are normally coherent. It is here, however, intended to apply it also to the abnormal dissociation of members belonging to different whorls; and the two cases will be taken together.

It is generally recognized that the dialyphyllous condition is more primitive than the gamophyllous, for the former is characteristic of those orders which in other respects are considered the more primitive; while those which exhibit gamophyllly are for the most part more advanced. As an example from each group respectively may be mentioned the Ranunculaceæ and the Campanulaceæ. Hence it may be here at once stated that all cases of dialysis affecting any given floral whorl are reversions to a more ancestral state.

(1) CALYX.

Gamosepaly and gamopetaly are nearly always associated; and where dissociation of the petals occurs in a gamopetalous flower it is generally at the same time accompanied by dialysis of the calyx. This occurs now and again in a good many plants. Masters.

mentions the genera *Primula*, *Symphytum*, *Gentiana*, *Campanula* (Pl. XXXIX, fig. 1), and others as showing it. In each of these the normal flower has also a gamopetalous corolla.

Partial dialysis of the calyx has occurred in *Primula sinensis*; the sepals thus separated were in all cases long-stalked and foliaceous.

All so-called "inferior ovaries" are here regarded as being enclosed externally by the basal portions of the sepals. In the case of the Umbelliferae the major part of the sepal is used up for this purpose; in the Rosaceae, with completely organized sepals above the "fruit," it would seem, at first sight, more natural, as Celakovsky and others maintain, that the sepals have been displaced into that position through a cupular upgrowth of the axis around the ovary. But, supposing fusion of the sepal with the ovary to have occurred, there is no reason why the upper free portion of the sepal could not have become reorganized into the constituent parts of sheath, petiole, and blade. For there are instances in which the same kind of change occurs, viz., where a leaflet of a compound leaf, usually perfectly simple, may assume the complexity of organization of an entire leaf. Good instances of this are seen in the aphyllia of the tree-fern (*Hemitelia*) and in the leaflets of the laciniated varieties of the elder (*Sambucus nigra*).

In abnormal cases the calyx tends to become dissociated from the ovary, and at the same time the latter often becomes superior. Such free sepals have been observed in Umbelliferae (Pl. XXXIX, fig. 2). In the proliferated pears, described on an earlier page, the bases of the sepals in one or more of the extra pears formed by proliferation tend to become separated out and individualized; the outline of each is distinct and clear (see Pl. XXVIII, fig. 2); this is not the case with the normal pear at all. Planchon describes an interesting phenomenon in the quince (*Cydonia*) which was surmounted by five more or less foliaceous sepals, the surface of the fruit having five distinct ridges, each

immediately below one of the five sepals, and with fairly deep furrows between them. He also points out that occasionally in the rose the fleshy inferior "fruit" completely disappears, and the sepals are then united by their somewhat swollen or fleshy bases, the pistils being superior. Masters figures a remarkable case in the apple in which the sepals are situated at the base of the carpels (Pl. XXXIX, fig. 3). Planchon comes, like Masters, Penzig, and others, to the conclusion that of these Rosaceous "fruits" both axis and calyx are component parts. The Schleiden theory, that they are composed purely and simply of the swollen cupular axis, is almost certainly erroneous.

Dialysis of the receptacle observed by Domin in *Potentilla aurea* has been referred to on a previous page.

Stenzel figures flowers of the snowdrop (*Galanthus nivalis*) with one or two sepals situated at the base of the ovary, and Celakovsky describes and figures a flower of the same plant with a double sepal one half of which was green-striped and decurrent down the ovary to its base.

Magnus mentions the insertion of a sepal at the base of the ovary in the orchid *Dendrobium Wallichii*.

A most interesting *Fuchsia*-flower came under notice, in which three of the sepals were partly foliaceous with the lamina on one side, decurrent part way down the petiole, which in its turn could be distinctly traced down the side of the ovary to the base of the latter. This may be taken as a partial reversion of the calyx to its ancestral position, and the fact just cited proves definitely that in the normal flower the bases or stalks of the sepals are adnate to the "inferior" ovary, which is not, therefore, really inferior at all, nor of axial nature, as is usually supposed. In fact, the "inferior" ovary is, wherever it may appear to occur, a figment of the academical botanist's imagination (Pl. XXXIX, figs. 4-6).

Velenovsky describes abnormal flowers of the willow-

herb (*Epilobium montanum*) in which calyx, corolla, and androecium were not only completely dissociated from each other, but were situated, in the one case at the base of the ovary, in the other a short way down it; in these last two positions they were of precisely the same vertical height as in the normal position; the superior ovary had also precisely the same appearance (hairy, etc.); these two facts, he thinks, force us to the conclusion that in the normal case the calyx, etc., have been carried up on to the top of the ovary, for if they enclosed it as an axial or leafy receptacle the hairiness of the ovary should disappear in the abnormal condition. This view is hardly acceptable to the present writer, who considers that fusion of the calyx, etc., with the ovary in the normal case must be admitted, for it is inconceivable that one set of floral leaves could be seated on the tips of another set, and the axial theory is unlikely from comparison with other cases of inferior ovaries (see above). Moreover, it is conceivable that the superior ovary and short hypogynous calyx, etc., of the abnormal flower could arise congenitally in those positions with all their previous characters intact, as these characters constitute a useful adaptation to the needs of the plant and the less advantageous intervening stages would naturally be omitted.

In a flower of the "geranium" (*Pelargonium zonale*) the spur of the posterior sepal was dissociated from the pedicel, with which it is normally fused, for a distance of several millimetres; this is a reversionary tendency; for in its near ally *Tropæolum* this spur is normally quite free.

(2) COROLLA.

There are a great many plants which exhibit either partial or complete dialysis of their gamopetalous corolla. Only two or three instances need be given. One of the best-known is that of *Campanula* in which the flower bears five perfectly free outspread petals

(Pl. XXXIX, fig. 1); the sepals are also free in the same way. The harebell (*C. rotundifolia*) has been found in the wild state with polypetalous flowers. Certain of the Ericaceæ, e. g. *Rhododendron*, *Rhodora*, *Erica*, occasionally exhibit a polypetalous corolla; this is not a surprising fact when we know that several genera of the order Ericaceæ possess this character normally, e. g. *Pyrola*, *Clethra*, *Leiophyllum*, *Ledothamnus*, *Cladothamnus*, *Elliotia*; so that, so far as this particular feature is concerned, these genera stand nearer to the ancestral form.

In the flower of *Stapelia*, previously described, in which an extra corolla appeared, the normal corolla was dialypetalous: a rare phenomenon in the Asclepiadaceæ.

In double flowers, where fresh petals are added from the andrœcium or are intercalated independently, it frequently happens, as in *Nerium Oleander* and *Oalgystegia pubescens* mentioned by Goebel, that, not only the newly-added petals but the normal ones as well, are polypetalous from the first. This is due, probably, to correlation of growth; we can understand that if the normal corolla had remained gamopetalous it would tend to cramp and hinder the expansion of the flower caused by the addition of new petals, while the polypetalous condition would not do so.

Celakovsky observed a most interesting variety of *Anthemis austriaca* in which the ray-florets were not, as in the normal form, ligulate, but bilabiate (Pl. XXXIX, figs. 7 and 8). As is shown by the nervation, the normal ligulate corolla, in spite of having a tridentate apex, really contains within itself all five petals. This is proved beyond all doubt by the organization of the floret in the variety, in which two lateral upper petals have become detached, and in many cases constitute an upper lip. The chief interest of this abnormality lies in the fact that the bilabiate character of the ray-florets is the normal feature in one section of the Compositæ (*Labiatifloræ*) to which the Mutisieæ

and Nassauvieæ belong. The abnormality in *Anthemis* is of the nature of a reversion towards a condition in which zygomorphism is not so pronounced as it is in that of the extreme ligulate type of ray-floret.

The corona of *Narcissus* tends to become partially or completely split up, especially in double flowers. This subject will be more fully referred to on a subsequent page.

(3) ANDRÆCIUM.

The possession ofadelphous stamens, in which a larger or smaller number are united for the whole or a portion of the length of the filaments, is a characteristic of certain orders. For example, the Malvaceæ, Leguminosæ, and Cucurbitaceæ. This is also a more lately acquired character.

When the balance of the plant becomes upset from whatever cause, inducing virescence and doubling, etc., there is nearly always the tendency introduced to revert in one or the other character to a simpler and more primitive condition. Thus it was found in plants of *Trifolium repens* whose flowers were afflicted with virescence in the pistil, that the column of nine stamens had become broken up into its constituent parts, all the stamens being separate and outspread.

A similar dissociation of the stamens composing the column of the Malvaceæ is a concomitant of doubling of the flower in many cases, as has been noticed in the hollyhock (*Althæa rosea*).

The stamens of the Fumariaceæ are for the most part diadelphous. In the transverse plane are two groups; each of these consists of a stamen of the outer whorl united on either side of it with a monothecal stamen from the inner whorl. Dissociation of these stamens has sometimes been observed, as in the interesting case mentioned by Wydler in the bleeding-heart (*Dielytra spectabilis*), in which all six stamens (metamorphosed into small foliage-leaves) were per-

fectly separate, and inserted in the flower as in the typical Cruciferous type.

In orchids the stamens become separated from the pistil of the column, which, of course, is a reversion to the original condition, as was seen in double flowers of *Miltonia vexillaria* in which the column was broken up into its constituent parts. The free stamens which then appear, at least in most cases, are the anterior one of the outer whorl (A^1) and the two anterior ones

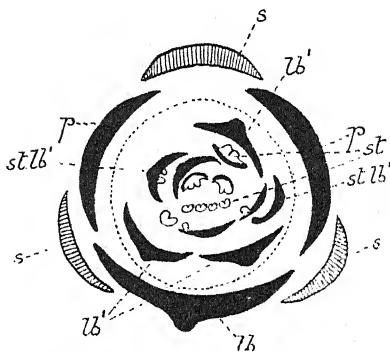


FIG. 113.—*Odontoglossum crispum*. Fasciated flower (in process of branching into a number of flowers) showing dialysis of the "columns" (more than one present). Pistil completely absent. (Diagram.) s, sepal; p, petal; lb, labellum; st. lb¹, labelliform stamen; st, stamen

of the inner whorl (a^1 and a^2). A similar phenomenon was seen in *Odontoglossum crispum* (fig. 113).

The most ancestral group of the orchids, viz., the Apostasieæ* (a tribe of the sub-order Diandræ), takes its name from the fact that the stamens are almost free from each other and from the style, the column being excessively short. We see here, in fact, the very earliest stage in column-formation in the order. Hence in this group we have a normal counterpart of what is occurring abnormally in the *Miltonia*.

Masters found dissociated stamens in some of the

* Rolfe gives a clear account of this group and the Cyripediæ, showing their relationship to each other and to the Monandréæ.

flowers connected with the abnormal cucumbers already cited.

In a proliferated floret of the goat's-beard (*Tragopogon pratense*) which had become virescent, the usually syngenesious anthers were quite free. In the normal floret of *Compositæ* and the flower of *Cucurbitaceæ* the anthers are postgenitally, not congenitally, united.

In the abnormal axillary "stamens" of *Euphorbia* described by Schmitz there were frequently present so many as four to six loculi, all of which he ascribed to the anther of a single terminal axial stamen. But Celakovsky points out that in *Euphorbia* there are really two stamens present, and an abnormality of Schmitz's shows this, although that author placed, as Celakovsky shows, a quite wrong interpretation thereon. In the axil of one of the leafy bracts was a structure consisting of two practically opposite foliar organs, one of which bore two interior pollen-sacs, and clearly represented a stamen; at the base of the other leaf occurred two minute leaflets, which Schmitz ascribed to the terminal bud of the whole axillary structure, but which Celakovsky says must represent the two pollen-sacs of the second leaf. If this, as is probably the case, is the right interpretation, then we have a dialysis of the "single stamen" into its two actual constituents, which are at the same time virescent.

In virescent flowers of *Lysimachia*, *Cyclamen*, and *Anagallis* it has been observed that the stamens become completely free from the petals and inserted on the receptacle; in otherwise normal flowers of *Primula vulgaris* and *P. sinensis* the same thing has been seen (Pl. XXXIX, fig. 9); this abnormality is of great importance as showing that the petal and its superimposed stamen are to be regarded as two distinct and independent foliar organs forming two whorls; it is quite antagonistic to the view of Duchartre and Pfeffer, founded on the altogether

deceptive data of the development, that petals and stamens in Primulaceæ constitute a single whorl.

This is an excellent example of how the ontogeny proceeds in exactly the opposite direction to the phylogeny. For that reason are the ontogenetic facts, in this case as in so many others, exactly the reverse of serviceable to the comparative morphologist. Teratological facts and comparative data are alone useful.

In other Gamopetalæ, such as *Antirrhinum*, the same abnormality has been seen. Henslow figures in the dark mullein (*Verbascum nigrum*), stamens inserted on the receptacle (Pl. XXXIX, fig. 10).

(4) GYNŒCEUM.

APOCARPY.—It is generally recognized that the most primitive type of pistil is the apocarpous one, such as occurs in the Ranales, Alismaceæ, and Rosaceæ, in which the individual carpels are separate and distinct structures. The syncarpous pistil in which the carpels are all laterally united to form a single structure, the compound ovary, is a more recently acquired organ.

Just as, under the influence of the upset of equilibrium of the plant's constitution, the adelphous andrœcium becomes broken up into its constituent parts, in the same way may the syncarpous ovary become similarly transformed, and there is no reason for regarding this as other than a reversion, or a tendency to reversion, to an earlier state.

In the fasciated flower of *Scilla nutans* above described, which was the equivalent of several flowers, and in which the stamens had mostly become petaloid, the carpels had nearly all become dissociated and were represented by a host of separate leaves, although there was also present an almost perfect trilocular ovary; these separate carpels bore anthers.

It is quite common for the ovary of the Cruciferæ to become resolved into its two component carpels, as

in the wallflower (*Cheiranthus Cheiri*) mentioned by Spinner.

Dissociation of the carpels ("quarters") of the orange and lemon gives rise, if it is partial, to the very curious fingered or hand-shaped fruits in which the carpels are still united at the base. Or, if completely separated, they may form, as in the semi-double flower mentioned by Duchartre, a whorl of eight to ten distinct carpels. When a second whorl of carpels is formed, as in the navel orange, the apocarpous condition is usually marked.

In an abnormal crocus-flower examined, the three styles, usually connate, were completely free and distinct.

Mr. J. Weathers sent a drawing of a pistil of *Lilium*, with three perfectly free styles, whereas, in the normal pistil, both styles and stigmas are intimately fused.

The five carpels constituting the ovary of *Primulaceæ* are so intimately united that there is no indication in the mature condition of its original constitution, there being a single style and no sutures on the surface of the ovary; moreover, in the development the structure usually arises as a uniform "ring-wall." Now and again, however, as observed for instance by Masters, the pistil arises as five distinct tubercles on the receptacle. Here we have one of the comparatively rare instances in which the ontogeny throws light on the phylogeny. In abnormal flowers, as seen for instance by T. G. Hill in *Primula*, some of the carpels composing the pistil become partially individualized in the form of two or three styles. Masters figures a pistil of *P. prænitens* with four styles and marginal ovules (Pl. XXXIX, fig. 11).

SOLUTION OF "INFERIOR" OVARY.—The solution of the carpels from the tubular calyx-base is undoubtedly of reversionary nature, and occurs frequently when the balance of the organism becomes upset, as in many abnormal roses, apple-blooms, hawthorn, *Umbelliferæ* (Pl. XXXIX, fig. 12), etc. Masters figures a beautiful

instance of this in the apple which is here reproduced (Pl. XXXIX, fig. 3). In such cases the characteristic swollen and fleshy base of the flower, viz., the "pome" or the "hip" completely disappears and the carpels occur in a perfectly superior position, in that position, in fact, in which they are formed in those plants which, on other grounds, are regarded as the more primitive. A study of the early development of normal flowers in the bud reveals the fact that the carpels arise at first in the superior position and at a later stage become depressed into the "inferior" one, hence the ontogeny is in this case a recapitulation of the phylogeny.

In a fasciated flower of the vegetable marrow (*Cucurbita Pepo*) the "inferior" ovary had completely vanished; a swelling at the base of the styles and above the insertion of the petals probably represented a rudimentary ovary.

But Masters gives a very striking instance in the cucumber (*Cucumis sativus*); in the secondary flowers, produced as a result of proliferation from the axils of the petals of the male flower, carpels occurred in a perfectly superior position amongst the stamens, and, further, these carpels were completely open, exposing the ovules attached to their margins, a fact which shows that the placentation in the Cucurbitaceæ is really marginal.

Begonia-flowers are very apt to show changes of this kind. One was observed in which the "inferior" ovary was almost extinct, and the styles were growing out of a large solid green mass in a "superior" position which was completely covered externally with ovules, and probably represented the greatly-swollen placental bases of the carpels.

In erect, more or less virescent flowers of the snow-drop (*Galanthus*), received from Miss Partridge, Hockham, Norfolk, the "inferior" ovary had disappeared and the carpels were represented by minute, colourless, imperfectly expanded and unfolded leaves, bearing

rudimentary ovules on their margins, and seated in the centre and base of the flower.

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ADDENDUM TO FASCIATION, p. 47.

In a fasciated flower of the common buttercup (*Ranunculus acer*) seated at the apex of a fasciated peduncle, one side was very much more advanced in development than the other, having large green ovaries around which all the stamens, petals, and sepals had fallen off, while on the opposite side all these members were present, and no trace of the pistil could be seen except in microscopic section, which revealed its very rudimentary state of development. This phenomenon was due to the unequal growth on either side of the peduncle, and consequently of the flower, and is, as described in Vol. I, a common accompaniment of fasciation.

6. METAMORPHOSIS.

It was C. F. Wolff who was the first to hint at the origin of the flower as being the outcome of a gradual metamorphosis of the foliage-leaves situated at a lower level on the axis of the plant. He held that the production of floral leaves was the result of a degeneration in the quality of the sap, the richer portion being used up at a lower level by the first-formed vigorous foliage-leaves. The great German poet Goethe, however, first established the theory of the underlying homology of all foliar organs of the plant. His main idea was that the floral leaves represent the final stage in a gradual ascending metamorphosis of which the foliage-leaves are the starting-point, and that the production of flowers is due to an improvement and etherealization of the sap during its ascent through the plant, all foliar organs being variants on an ideal type-leaf. This conception was probably the best that could be framed at a period when our modern idea of descent with modification from some one primitive form was conspicuous by its absence. These two great thinkers dealt solely with the individual development of the plant; they, like so many biologists since their time, failed to see that this could throw no real light upon the ultimate phylogenetic development of the parts concerned. Goebel holds that any foliar organ of a flower, whether sepal, petal, stamen, or carpel, is a modification or transformation of a rudiment, which itself is always of the nature of a foliage-leaf. Celskovsky derived both perianth- and foliage-leaves from sporophylls.

The majority of modern botanists hold that the process during the evolution of the race has been that which Wolff and Goethe set forth, although these writers had an eye on the process of individual development only; viz., that the flower as we know it in the

Angiosperm has been evolved out of an elongated shoot bearing well-developed foliage-leaves which were in part fertile. This view was probably originally founded on teratological data; sepals, petals, stamens, and carpels were observed to frequently change into foliage-leaves; but partly, perhaps, on facts of ontogeny, in which the rudiments of both floral and foliage-leaves were seen to arise and develop in the same way. But there is no value to be attached to this last fact. Floral leaves must be supposed to arise congenitally as such; a stamen is a stamen and nothing else from its birth onwards, and there is no evidence that in the ontogeny it passes through any foliage-leaf stage. Hence Goebel must be held to be in error in ascribing, without adducing any evidence, foliage-leaf nature to every rudiment of a floral leaf. The rudiment is, admittedly, a plastic structure, and may, under certain conditions of nourishment, etc., be capable of developing into a foliage-leaf. In fact every floral leaf may be regarded as having the potentialities of every other and of a foliage-leaf; but that is a different thing from assuming that foliage-leaf nature must still inhere in every floral leaf in the earliest stage of its ontogeny, for this implies a denial of its congenital value as a floral leaf.

We have in the last few years had strong grounds for holding the view that both recent and Mesozoic cycads have been derived by descent from the Pteridosperms of the Coal Period. The latter possessed sporophylls of, for the most part, great complexity, fern-like in organization, and in some cases, either in whole or in part, foliaceous and assimilating, like the sporophylls of modern ferns. It is probable that the shoots bearing sporophylls of this nature are the actual progenitors of the flowers or cones of the Mesozoic and recent cycads. The sporophylls became very greatly reduced in complexity of organization and in size. The excessively simplified male and female sporophylls (stamens and carpels) of a modern cycad, or the female

sporophylls of *Bennettites*, would never be recognized as, or credited with, having such an ancestry in the past, if the ulterior facts were not known. But in the male sporophylls of *Bennettites* (*Cycadeoidea*) we see an interesting transitional form between the ancient and the more modern type of sporophyll, for these structures still retain a somewhat fern-like organization of leaf, although they are, like the sporophylls of so many Angiospermous flowers, arranged in a whorl.

It is, therefore, practically certain that in the Pteridosperm-Cycad phylum we have an objective case before us of the evolution of the flower- and cone-structure from an elongated leafy shoot; *i. e.* of the shoot becoming congested, and the leaf-like sporophylls becoming reduced and simplified to the modern cycad-sporophylls, and crowded in dense spirals or in whorls on the shortened axis. If this is true of the flowers and cones of the cycads, it must be equally true of the very similarly organized flowers of the Angiosperms.

After these introductory remarks on the evolution of the flower the facts of its abnormal metamorphogenesis will be set forth. The phenomena are best classified under the headings of the various types of floral leaves.

Before considering the various changes which affect the different kinds of floral members attention may be directed to the types of change induced in all the organs of the flower at the same time and in the same way.

PHYLLODY.—The phenomenon which many authors have named "chloranth" consists in the transformation of all the floral leaves into foliaceous structures. The best-known example of this is the "green rose," a frondescent variety of the monthly rose (*Rosa indica*); here sepals, petals, stamens, and carpels are in the form of green leaves; but these are small in size and simple in conformation, and do not in any way resemble the ordinary foliage-leaves of the plant. Magnus mentions that a flower of *Anemone ranunculoides* attacked by the

Urédineous fungus *Æcidium punctatum*, was in the form of two green leaflets, one of which was palmately divided.

Flowers of *Saxifraga Cotyledon* were seen which were represented by a rosette of five green leaves (Pl. XL, fig. 1).

Harshberger observed, in an abnormally-branched inflorescence of Venus' fly-trap (*Dionæa muscipula*) the development of long-stalked rosettes of foliage-leaves.

Seringe describes a flower of the wall-mustard (*Diplotaxis tenuifolia*) in which each of the sixteen floral organs was in the form of a green leaf. Pl. XLI, fig. 4, shows two flowers changed into leafy shoots. The Cruciferae are much liable to this change in their flowers. There may here be cited the case described by Wigand of the flote-grass (*Glyceria fluitans*) whose flower had its paleæ, lodicules, and stamens represented by ligulate leaves. This is merely an early stage of the condition in which the flower is constantly and normally replaced by a completely-formed leafy bud, giving rise to vivipary. Penzig observed flowers of the Indian cress (*Tropæolum majus*) in which every member of all whorls (including ovules) was transformed into a stalked, peltate foliage-leaf.

The above-described phenomenon may be termed "phyllomania."

BRACTEODY.—There are other cases in which all organs of the flower are changed into structures which must be regarded, from their size and shape, as bracts rather than foliage-leaves; owing to the elongation of the axis, their number is at the same time greatly increased. Such are the wheat-ear carnation, the Cornish and cross-leaved heaths (*Erica vagans* and *E. Tetralix*), the Madonna lily (*Lilium candidum*), and the snowdrop (*Galanthus nivalis*) (fig. 114).

In *Juncus lamprocarpus* an inflorescence was seen transformed into a kind of very compact rosette of large bracts (Pl. XLI, figs. 2 and 3).

This phenomenon is termed "bracteomania."

SEPALODY.—There is a second type of wheat-ear carnation, sent by Mr. Chittenden, in which the leaves composing the entire structure are, to judge by their larger size and relatively greater breadth, sepals and



FIG. 114.—*Galanthus nivalis* (Snowdrop). Virescent flower (on right) showing the following changes: All floral members transformed into greenish leaves; "inferior ovary" absent owing to solution of perianth-leaves therefrom; the pendulous flower has become erect. A normal flower (on left) for comparison. (Mingay photo.)

not bracts. The whole structure is also much less elongated and much greater in diameter (Pl. XLI, fig. 1).

Rendle describes flowers of the fine-leaved heath (*Erica cinerea*) which consisted of nothing but great numbers of red foliar organs which were probably sepals.

The changes which each type of floral leaf undergoes will now be considered.

(1) CALYX.

PHYLLODY.—This includes those cases in which sepals become foliaceous.

The change may be very slight; in some flowers of *Clematis viticella* some of the white petaloid sepals were slightly virescent near the apex; other sepals were green throughout, except along the two basal margins. In some of the sepals the change was complete to a ternate foliage-leaf. In another species (*C. Fortunei*) the change was not nearly so complete, the leaves being "simple."

In the tulip the three sepals have been observed quite green, as they normally are in the Commelynaceæ.

In some flowers of *Primula sinensis* the upper surface only of the enlarged sepals was virescent. In some other flowers of this plant received from Mr. Odell the calyx had become foliaceous, although in most of them the sepals remained united into a tube below; here and there, however, a sepal was quite foliaceous, having a long petiole; in all these cases the zygomorphism of the calyx was much more marked than in the normal flowers, and the posterior sepal larger than the rest. The polyanthus (*P. vulgaris* var.) often shows a leafy calyx (Pl. XLVII, figs. 1-5).

In the rose it is frequent for the sepals to be congenitally transformed into well-developed foliage-leaves. Transitional forms show that the normal sepal does not correspond to the leaf-base, but to the entire leaf. Pl. XLII, fig. 1, shows a flower, similarly transformed, of a laciniated variety of the blackberry (*Rubus fruticosus*); in correlation with this remarkable change, the corolla has become completely suppressed.

In *Helenium autumnale* and the goat's-beard (*Tragopogon pratense*), belonging to the Compositæ, the pappus (calyx) of the florets has been seen changed, in the

former case into two to eight, in the latter into two to five narrow green leaves (Pl. XL, figs. 2 and 3), a very interesting reversion to the ancestral condition. It was due to the capitula being infested by a mite (*Phytoptus*).

Magnus describes flowers of *Anemone ranunculoides* attacked by the Uredineous fungus *Æcidium punctatum* in which the perianth-leaves had become foliaceous or virescent.

In the primitive order Ranunculaceæ some of the genera normally possess petaloid calyces, e.g. *Helleborus* sp., *Anemone*. Velenovsky figures an abnormal flower of the wood-anemone (*A. nemorosa*) with three inner coloured leaves (best regarded as petals) and three outermost, perfectly green, and smaller sepals. In another flower figured by him there is an inner whorl of six narrower and an outer of six broader leaves, but all are similarly coloured. Here we get a distinct differentiation, in the first case greater, in the second smaller, into two divisions of the perianth; in the first-mentioned instance the three outer green leaves may be compared to the trifoliate green calyx of the lesser celandine (*Ranunculus Ficaria*). Such a case throws a distinct light upon the origin of the calyx in flowers generally. Here we have, in an abnormal example, a green calyx which has been derived directly from a petaloid one.

Prantl, Goebel, Velenovsky, and others hold that the calyx is phylogenetically bracteal in origin, a view derived probably from the fact that the calyx is usually green and leaf-like, and often differs from the corolla in displaying a spiral arrangement of its sepals. Velenovsky brings forward the examples of *Camellia*, *Cryptandra*, etc., to show that the sepals here belong to the same spiral series as the numerous bracts below them and therefore must have been derived from them. This phenomenon is also very obvious in the Japanese allspice (*Calycanthus*).

The view of Celakovsky, however, here supported, is that the calyx is in all cases a derivative, like the

corolla, of the andrœcium. It is quite likely that in *Calycanthus*, *Camellia*, *Cactaceæ*, etc., the bracts also have been derived from the stamens; though it is possible that they have been derived from foliage-leaves and have later come to arrange themselves in the same spiral series with the floral leaves; or, what is perhaps more likely, of the self-same bracts, some have come from the calyx and some from the foliage-leaves.

The facts of floral morphology in the *Ranunculaceæ* strongly support the view of the staminal origin of the calyx. The presence of a petaloid calyx when the corolla is absent or represented by staminodes or nectaries, and the fact that staminodes and nectaries are of earlier origin than coloured petals, because more nearly related to stamens and derived from them, shows that the petaloid calyx (the almost constant concomitant of the staminodes, etc.) must be of earlier origin than the green calyx of the buttercup (*Ranunculus acer*), etc., and that of most Dicotyledons.

The following remarks on the genus *Anemone* from another publication by the present writer may be of interest: "In some species, as *A. virginiana*, *A. pennsylvanica*, and *A. ranunculoides* there is a single perianth-whorl of five coloured leaves, these being arranged, as in *Caltha*, etc., in a spiral; the perianth is in this case, as in the other genera above-mentioned, obviously a calyx. In other species, as *A. hortensis*, *A. nemorosa*, *A. Halleri*, there is a distinct tendency shown towards the arrangement of the sepals in two distinct whorls, while at the same time one or two 'extra sepals' have been added above, with the result that there obtain, as in *A. nemorosa*, two whorls of three or four members each. *A. sylvestris* affords a transitional case, where the five sepals are, as it were, hesitating whether to be whorled or spirally arranged on the axis.

"Now consider the very striking case of *A. japonica* or of *A. stellata*. Here, to the original and primitive

* The writer now holds that all perianth-leaves above the five outermost are best regarded as petals.

5-merous calyx, a considerable number of members have been added, so that the perianth frequently consists of so many as twenty sepals,* and it is, moreover, clear that these have been added from the stamens, by their metamorphosis, for, in the centre of the flower, transitional forms between stamens and sepals are always present, and we receive, as it were, ocular demonstration of the method of production of these sepals which from without inwards form a continuous spiral of similarly-constituted petaloid leaves. But the most important fact has yet to be stated. In *A. japonica* two or three of the outermost sepals (as is also the case in *Trollius*) are always slightly differentiated from the rest, owing to their having, in whole or in part, a somewhat darker, purplish coloration, and occasionally they exhibit a decidedly greenish tinge. Now, in that section of the genus known as *Knowltonia* (exhibiting also a polymerous calyx) these *two or three outermost sepals are entirely green and bract-like*. Prantl accounts for the polymerous perianth of these forms by assuming that the single perianth of other species (which, on his view, is of bracteal origin) first multiplied its parts and subsequently became differentiated, as regards colour and texture, into two distinct portions. But, as Celakovsky aptly suggests, this multiplication could hardly have taken place *ex nihilo*; on the contrary, the extra sepals must necessarily have been derived by metamorphosis of the stamens [and it may here be added that multiplication of the perianth by division of its leaves (positive *dédoublement*) is most unlikely to have occurred, for the trend of floral evolution has been quite in the other direction, viz., by fusion and abortion of members], and further, if the perianth be originally of bracteal derivation it would seem strange that single perianths of a green bract-like consistence are of such rarity in the order." In *A. japonica* the outermost two or three perianth-leaves are, in many cases, of the same colour and texture as

* See footnote on p. 128.

those further to the inside which are formed from the stamens; they are also approximately of the same size, and are in the same spiral series. These facts being so, is it likely that these two or three outer sepals have had a different origin from the innermost ones?

In *Salix* the perianth (calyx) is in the form of mere glands; Celakovsky saw these in "a quite leafy" condition; Hegelmaier observed them united to form a kind of lobed ring.

BRACTEODY.—The tendency in both floral and vegetative shoots is to form new organs from above downwards; it is rarer for foliage-leaves or bracts to be carried upwards by suppression of internodes or otherwise. Hence the bracts of *Anemone* and the tulip are here regarded as having been derived from the calyx. In the tulip we constantly see a sepal displaced downwards (by development of an internode) and becoming foliaceous, while its place is taken by a petal, whose place in turn is filled up from the andrœcium; this process involves an upset of the cyclic arrangement and consequent twisting of the peduncle. In support of this view it may be mentioned that in a plant of *Anemone coronaria* var. *chrysanthemiflora* which was observed in Kew Gardens there was an extra whorl of three foliaceous bracts immediately above the normal one; in other flowers the foliaceous bracts of the extra whorl are represented by petaloid leaves; or these leaves may form part of a third whorl slightly higher up still. Now, it is clear, or at least, very highly probable, that these extra whorls of bracts have been derived directly from the calyx, within which is a well-nigh inexhaustible supply of stamens; while it is very difficult to imagine how this entire involucre system could have been projected upwards from that of the foliage-leaves, the number of which is extremely limited. If this is the case, then we must regard the normal trifoliate involucre as having also a floral origin, and not regard the calyx as having been derived from the involucre.

The resemblance, alike in number, size, consistence, and position, of the bracts of *Hepatica* (often placed in the genus *Anemone*) to the sepals of *Ranunculus Ficaria* would strongly suggest a common origin for the two; and if the calyx of some Ranunculaceæ, e. g. *Anemone* (to which *Hepatica* is closely allied), is most probably staminal in origin, the same origin must be ascribed, directly or indirectly, to the calyx of all other members of the order*; and hence it is most likely that the bracts of *Hepatica* are staminal in origin, and are not in process of giving rise to a calyx. Celakovsky mentions that occasionally a fourth innermost bract is added to the involucre of *Hepatica* by transformation of the first or outermost sepal.

It was observed in the marsh-marigold (*Caltha palustris*) that one of the sepals had become displaced down the peduncle for a distance of a quarter of an inch, leaving a gap in the calyx; it still retained its yellow colour and consistence.

Here also may be mentioned an example, received from Dr. Salisbury, in which one of the sepals of a flower of the harebell (*Campanula rotundifolia*) had become displaced $1\frac{1}{4}$ inches down the peduncle, leaving a gap in the calyx; it had also assumed the size and shape of a foliage-leaf.

Both these last phenomena may be regarded as of the nature of attempts to form bracteoles.

These facts certainly seem to support the view that bracts (or bracteoles) have been (in the above cases at any rate) derived from sepals. This deduction will thus help to explain a phenomenon observed recently in a tulip-flower which consisted of the carrying-up of two bracts (by fusion, apparently, of their bases with the peduncle) to form part of the calyx. This may be regarded as a reversion, the bracts simply returning from whence they came. It can hardly be

* Celakovsky describes and figures flowers of *Ranunculus Ficaria* in which two extra sepals, making five in all (cf. *Ranunculus acer*, etc.), had been added by transformation of the petals.

held that the reverse phenomenon was occurring, viz., that bracts were being formed from the calyx, for the number of stamens had increased from six to eight, indicating that it had been found necessary to transform two inner perianth-leaves (corresponding to the two extra sepals derived from bracts) into stamens. The extra stamens cannot otherwise be accounted for.

HETEROSEPALODY.—In some zygomorphic flowers there are two kinds of sepals in the flower: the ordinary ones and those which are spurred. The

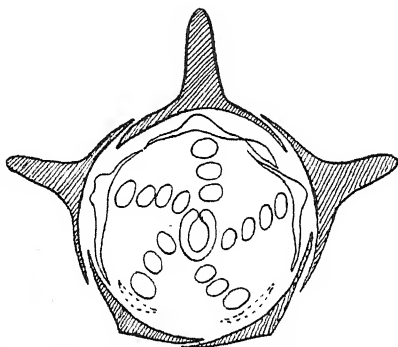


FIG. 115.—*Delphinium Ajacis* (Annual Larkspur). Flower with two extra sepal-spurs. Diagram. (After Braun.)

abnormal change consists in the metamorphosis of one kind into the other.

Spur-formation.—In *Delphinium*, e. g. *D. Consolida*, the posterior sepal only is normally spurred; in abnormal flowers one or more extra sepals may be spurred (fig. 115), even all five sepals may be spurred. Just the same kind of change may occur in the monkshood (*Aconitum*). In the Indian cress (*Tropæolum majus*) two spurs were seen; they were situated between the posterior and lateral sepals; normally there is a single spur in the median posterior position, which is often regarded as being formed by the whole of the median and by half of each lateral sepal, hence the phenomenon just mentioned may be due to the

division of the normal one, the products belonging to the posterior half of each lateral sepal. Buchenau described 3-spurred flowers (fig. 116). In the vast majority of cases he observed that the presence of extra spurs was correlated with the complete absence of a bract. In some cases the extra spur or spurs were turned inside out and solid. In a 4-merous flower, in which the sepals were diagonally placed, he found the single spur placed opposite the posterior petal. Such anomalous positions for the spurs as he repeatedly

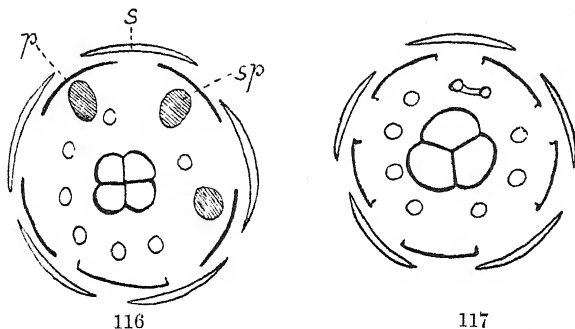


FIG. 116.—*Tropaeolum majus* (Indian Cress). Flower with three spurs (sp) opposite the petals (p); s, sepals.

FIG. 117.—*Tropaeolum majus*. Peloric flower; no spur present.
Diagrams. (After Buchenau.)

describes in his paper, as in the last-mentioned case and the one seen by the present writer, may probably be accounted for by the fact that the three posterior sepals completely dominate that region of the flower; the posterior portion of what appears to be the receptacle really represents the fused basal portion of the three sepals, and its coloration is the same; and as the insertion of the posterior petals is a very slender one the basal spur-bearing portion of the calyx may actually overlap the petal-insertion, as would seem to be the case in Buchenau's 4-merous flower. Such a condition of affairs would fully explain the abnormal position of the spurs. In any case the view held by Buchenau, Dammer, and others, that the spur repre-

sents an excavation of the receptacle (!) cannot here be followed. If it were so that would indeed be an anomaly in the vegetable kingdom, for no parallel case to a phenomenon of that kind can anywhere be found. That the spur is really part of the posterior sepal is shown by *Pelargonium*, a near ally of *Tropæolum*, in which the spur is undoubtedly an outgrowth of this sepal.

In *Pelargonium*, besides the posterior sepal (no. 2 in the order of development), sepals 1 and 3 have also been seen spurred.

Where all five sepals, as in *Delphinium* and *Aconitum*, are spurred, we have "true pelory," *i. e.* a change from the irregular or zygomorphic to the regular or actinomorphic flower, for it is to the presence of a spur in one of the sepals only that the zygomorphic condition is due.

Then there are the rare cases in which spur-formation occurs in the calyx, where, under ordinary conditions, this whorl is quite devoid of such structures.

Sommier and Hemsley describe spur-formation in the lateral sepals of a butterfly-orchis (*Platanthera chlorantha* var. *tricalcarata**) (Pl. XIII, fig. 2).

Loss of Spur.—The converse change occurs when the posterior sepal completely loses its spur, so that it comes to resemble the remaining sepals. Here we see a second type of "pelory." This has been noted in *Delphinium*, *Aconitum*, *Pelargonium* (a terminal flower), the canary-creeper (*Tropæolum aduncum*), and *T. majus* (fig. 117). In these the flowers were either terminal or lateral; in the first-named species some of the flowers remained partially irregular owing to lack of modification of the corolla.

Zygomorphy.—Hildebrand and Vidal both observed remarkable, irregular flowers of *Fuchsia* in which, along with other changes in the corolla, the posterior

* Phenomena of this kind represent what is known as "false pelory," because the foliar organs which take part in it are not all of the same kind (in this instance two sepals and one petal).

sepals became enlarged, or, at the same time, leafy, and formed, with or without the petals, a kind of helmet. The flower was obliquely-ascending in position (Pl. XLII, fig. 3).

PETALODY. — This phenomenon, sometimes called "calycanthemy," occurs, as we have already seen, normally in certain orders, *e. g.* Ranunculaceæ, as in *Hepatica* and *Delphinium*; and in *Ribes*, *Fuchsia*, etc. Often also the calyx is correspondingly enlarged, as in *Mussenda* and the milkwort (*Polygala*). As examples of abnormal petalody of the calyx can be mentioned the "hose-in-hose" primrose, and a similar "sport" of *Mimulus*. The garden variety of *Rhododendron indicum* known as "*Azalea amoena*" is characterized by having the same hose-in-hose conformation, and it is this, doubtless, to which it owes its specific name, for this feature makes it exactly twice as gay and beautiful as the normal form. Amongst the best-known cases of petalody of the calyx are those of the peach-leaved bell-flower (*Campanula persicifolia*) and the Canterbury bell (*C. Medium*), the coloured gamosepalous calyx, being widely outspread, giving some reason for the popular name "cup-and-saucer." Whether cases like this are to be regarded as reversions it is impossible certainly to say; they surely tend to support the view expressed on an earlier page that calyx and corolla have a similar origin; but this interpretation may clearly be applied to the instances of goldielocks (*Ranunculus auricomus*), etc., where some or all of the sepals become petaloid, for the majority of this order have petaloid sepals.

In certain orchids similar changes occur: Masters observed that in *Cattleya Trianae* the median sepal had assumed the form of an ordinary petal; flowers of the man-orchis (*Aceras anthropophora*) have been seen with labelliform lateral sepals. Penzig noted the same phenomenon in the green-winged orchis (*Orchis Morio*).

In *Orchis laxiflora* and *Serapias cordigera* it was seen

that half of each lateral sepal nearest the labellum was labelliform. This phenomenon was also observed in *Cattleya labiata*.

Forms of the snowdrop (*Galanthus nivalis*) have been seen in which all six perianth-leaves had the form and coloration of the petals, due to petaloid transformation of the usually white and larger sepals. The Sachsian explanation of these cases of the orchids and snowdrop, adopted by Goebel and others, is surely no explanation at all; the same material which normally goes to the building of a petal only has in these cases also been employed for that of a sepal, hence the petaloid appearance of members of the outer whorl; but this proposition merely suggests the further question: what has directed this inflow of petaloid material into the outer whorl? and we are just where we were before!

Petalody of the calyx seems to indicate community of origin of calyx and corolla, viz., from the androecium; that petal and sepal are one and the same organ; and in this sense the phenomenon may be regarded as a reversion from the more recent differentiated condition.

STAMINODY.—This is much rarer. Gris records an instance of a flower of the mock-orange (*Philadelphus speciosus*) in which one of the divisions of the calyx bore an anther-loculus. A flower of the Dutch clover (*Trifolium repens*) was seen in which one or two of the semi-petaloid sepals bore anthers; also tulips in which most of the sepals had lateral lobes (of which more hereafter) and one of them bore a fertile anther; similarly-lobed sepals were seen in *Crocus zonatus*. For reasons which will appear later these lobed perianth-leaves of the tulip and crocus are here regarded as partial, imperfect reversions to the stamens from which they originally sprang.

Magnus observed fusion of the odd sepal with the "column" in the orchids *Cattleya labiata* and *Trichopilia tortilis*; he attributes this to the pressure caused by the fused perianth-bases in the bud; but this would hardly occur unless there was an innate tendency, due

to the original staminal nature of the sepals, to fuse with the "column." Hence this may be included under "partial staminody."

The cases of staminody, somewhat uncommon though they are, certainly support the view that the sepals have been derived from stamens, and they therefore represent reversions.

CARPELLODY.—This is perhaps somewhat more frequent. Laxton observed a flower of the garden pea (*Pisum sativum*) in which some of the segments of the calyx of a second flower, formed by proliferation within the normal one, bore imperfect ovules on their margins and their tips were prolonged into styles. It is not rare for the sepals of the tulip and crocus to become partially carpeloid, bearing ovules on their margins; in these cases all transitions have been found between carpels and sepals. These phenomena cannot be held to be cases of direct reversion. But on the view that the calyx has been derived from stamens, and that, moreover, as we shall see later on, the latter have a very close affinity, and are often interchangeable, with carpels, they may be regarded as cases of very indirect reversion.

(2) COROLLA.

PHYLLODY AND VIRESCENCE.—In *Primula sinensis* the petals showed but a slight change in this direction, being slightly enlarged and their upper surfaces green. In the primrose (*P. vulgaris*) flowers were seen whose petals were of the normal size but quite virescent: all of a yellowish-green colour, the stamens being, in correlation therewith, degenerated (Pl. XL, fig. 4). Flowers of the honeysuckle (*Lonicera Periclymenum*) and florets of the *Helenium* above described, have been affected in the same way. In *Begonia Pearcei* one petal was half-, the other completely virescent. In *Cattleya Loddigesii* all the perianth-leaves, except the lip, were in the form of narrow, virescent leaves, the flowers so affected being greatly dwarfed. Much the

same thing had happened to the perianth-leaves of a snowdrop (*Galanthus nivalis*) which had also become erect instead of spreading, and there was no difference either in shape or colour between those of the inner and outer whorl.

As in the case of the calyx, according to the degree of change will be the greater or less resemblance of the modified petals to the foliage-leaves of the same



FIG. 118.—*Rosa damascena* (Garden Rose). Showing normal calyx (*ca*), phylloidy of petals (*p*), and proliferation into a secondary flower (*fl²*). (Mingay photo.)

plant. The instances given above represent merely early stages in this change, which is usually spoken of as "virescence." As Masters points out, this term must be also applied to such cases as that of the "nasturtium" (*Tropæolum majus*) in which the frondescent petals had not the peltate form of the foliage-leaves, but were spatulate, though with long stalks; but in other cases their venation was more like that of true leaves than of petals. The petals of Cruciferæ, as Tubeuf mentions, often become green and much

altered in shape when the flowers are attacked by the fungus *Cystopus candidus*.

In a rose all the petals save one have been transformed into ternate foliage-leaves, and the stamens were changed in a similar way; the calyx was normal. The flower had proliferated to form a second flower whose calyx merged imperceptibly into the virescent superior carpels of the primary flower (fig. 118).

SQUAMODY.—In some flowers belonging to virescent heads of *Trifolium repens* the petals had become reduced to membranous scales, a feature in correlation with the leafy development of the carpel.

SEPALODY.—This is not common. A very good instance appears to be that of the St. Valéry apple, in which true petals and stamens are wanting, and the whorl of leaves succeeding and alternating with the calyx resembles it in the texture, colour, and size of its members, these acquiring the same fleshy basal portions, which fuse together and adhere to the extra whorl of carpels. That this is the true interpretation of the St. Valéry apple seems indicated from what was observed in a seedless Colorado apple which was wide open at the top, in this feature, as well as in the phenomenon about to be mentioned, being unlike any other apple ever seen. Alternating with the five sepals were five apparently partial tiny apples, each topped with a sepal. These must be regarded as the five petals transformed into sepals, each with its fleshy swollen base. Fig. 119 is from a photograph received from Mr. Watson, Curator of Kew Gardens. Special attention may be drawn to the important bearing of this interesting phenomenon on the true interpretation of the normal pome-fruit. It shows clearly that the outer fleshy part really consists of succulent foliar bases. The fruit under consideration differs from the St. Valéry apple (1) in the succulent petal-bases remaining free and unfused; (2) in the fact that the stamens do not become changed into carpels; and (3) in the fruit being seedless, and open at the top.

Caspary observed in several species of the white water-lily (*Nymphæa*) that the bract supplying the place of the anterior sepal, along with the two lateral sepals, became displaced downwards on to the peduncle, leaving only the single posterior sepal over for the flower. As a result of this and to supply a fresh calyx, the four diagonally-placed petals of the first whorl became transformed into sepals.

Celakovsky aptly points out that the flower of *Nymphæa* is one of the best for showing how, by means

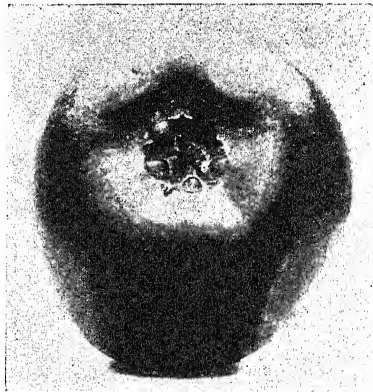


FIG. 119.—*Pyrus Malus* (Apple). Petals transformed into sepals, each with a fleshy base (= segment of apple-flesh).

of the excellent transitions which exist, the petals are all derived from stamens. In Caspary's abnormal flowers, therefore, we have a good instance of how sepals also ultimately have the same origin as petals, viz., from the stamens.

The origin of a whorl of sepals from a corolla-whorl as a normal process is most admirably exhibited by the Cruciferæ; as Celakovsky points out, the inner (transverse) calyx-whorl has here been derived by metamorphosis from the outermost corolla-whorl of the Papaveraceæ. For the Cruciferæ are a more recent, derived type than the Papaveraceæ, which come

very close to the Polycarpicæ, having a perianth composed of three whorls of two or three (often in *Papaver orientale*) members each, of which the two inner ones are petaloid and the outermost is sepaloid. In the Cruciferae the extra petals were subsequently added by positive dédoublement of the two median petals of the inner whorl.

A rather remarkable form of sepalody occurs in the double spurless variety of the columbine (*Aquilegia vulgaris* var. *stellata*), in which the usually spurred petals become replaced by spurless, flat, sepal-like leaves.* Transitions have been observed, moreover, between these two types of floral leaves. Both are equally derived by metamorphosis of stamens, and this affords another striking proof of the common origin, viz., from the andrœcium, of both calyx and corolla.

Celakovsky mentions that occasionally the two outermost petals of the lesser celandine (*Ranunculus Ficaria*) become transformed into sepals, so that a 5-merous calyx of normal orientation is thereby formed, leaving five petals out of the original eight, and bringing this plant in that respect into line with *Ranunculus acer*, etc. In other cases extra petals were added from the andrœcium to supply the place of those passed outwards (Pl. XLII, figs. 6 and 7).

There are varieties of *Iris Kæmpferi* and *I. Sieboldii* in which the inner perianth-leaves or petals, instead of being erect and of a different colour, are precisely similar to the sepals in their colour, shape, and position.

C. de Candolle, as previously described, mentions the appearance of an extra set of pappus-hairs in the Edelweiss (*Leontopodium alpinum*); as he observed transitions between extra corolla-lobes and pappus-hairs, we must probably ascribe the phenomenon to sepalody of the corolla; but a most unusual and remarkable case thereof.

* But all but the five outermost members of the flower are best regarded as petals.

When the corolla comes to resemble the calyx it must represent a further differentiation away from its original staminal structure, and hence this must be held to be a progressive phenomenon.

All these instances support the view that sepals and petals are essentially the same organs and have had an identical origin.

HETEROPETALODY. — Under this heading must be ranged those cases in which, in flowers normally producing more than one kind of petal, the one kind changes into the other; also those in which the petals become changed into a form not normally found in the genus.

In certain varieties of marguerite (*Chrysanthemum frutescens* var.) and *Pyrethrum* the disk-florets of the head become enlarged and coloured white like the ray-florets, this representing a half-way stage towards complete "doubling" of the head in which the further character of zygomorphy is added to the disk-florets.

In the snowball-tree (*Viburnum Opulus* var. *sterilis*) all the interior flowers of the corymb have become enlarged and white in colour like the peripheral ones, which gives the striking, showy character to the inflorescence of this variety. Now this feature, in which all the flowers of the corymb are alike, is the normal one in other species, *e. g.* the laurustinus (*V. Tinus*) and *V. macrocephalus*, although in these cases, of course, none of the flowers is sterile.

The same phenomenon occurs in certain garden varieties of *Hydrangea*, the interior flowers of the corymb becoming as showy as the exterior ones.

Labellum-pelory. — In orchids there are two kinds of petals: the ordinary, lateral ones, and the posterior median "labellum." The peculiar form of this latter is held by some authorities to be due to the lateral fusion with the original ordinary petal of the two lateral stamens of the outer whorl. Rolfe describes a flower of *Cattleya labiata* having an extra lip in place of one of the lateral petals, this being supposedly due

to the fusion of the anterior stamen of the outer whorl (A_1) with the petal, for this stamen is absent from the column. In a flower of *Cypripedium insigne* the two lateral stamens of the inner whorl (a_1 and a_2) were absent, and the lateral petals were transformed into labella (Pl. XL, fig. 5). In these we see, apparently, the labelliform character of the petal resulting from the fusion with it of a stamen. Yet it is doubtful if there is any real evidence in favour of the view that the labelliform character is due to the incorporation of stamens with a petal.

Dendrobium nobile var. *Cooksonianum* produces flowers in which the lateral petals are transformed into labella, or at any rate resemble them in most particulars. In a "spike" of another variety of this species all the flowers of one side were normal, while those of the other side had labelliform petals; in one of the flowers one of the petals retained its normal form and colour. In both varieties of *Dendrobium* the "column" was perfectly normal; hence there can be no possible question of anthers fusing with the petals to form the labella. Examples of this kind tend clearly to show that labellum-formation is an ordinary form of heteropetalody, comparable to the change of one perianth-leaf into another, either of the outer or inner whorl.

Theory of the Labellum.—The points brought forward in favour of the Brownian and Darwinian hypothesis for the origin of the labellum, viz., by the incorporation of stamens with an ordinary petal, are the following:

1. The vascular cords which correspond to the two stamens A^2 and A^3 pass, in many orchids, into the lateral regions of the labellum. This, however, is of no final value, for in other orchids the same cords are seen to be attached to those supplying the column. Moreover, the position of vascular strands cannot be allowed to be a factor in solving morphological problems.

2. In cases where the labellum is suppressed, or in the form of a lateral petal, stamens A^2 and A^3 sometimes reappear. But this is far from proving that they were ever fused with the labellum. Moreover, in the second alternative the change is merely that towards the primitive, regular flower, as in *Apostasiae*, and in the first alternative the change can be explained along the lines of correlative development of organs.

3. Magnus describes a flower of *Orchis papilionacea* in which anther-formation occurred on either basal edge of the labellum in most of the flowers of an inflorescence. This case is certainly in favour of the popular hypothesis. It would seem, however, to be the only one known of the same nature. It can quite well be interpreted in another way, viz., as a partial reversion, such as we so often see in petals, to the original staminal nature of the whole labellum. Both His and R. Brown describe transformation of the petals into stamens.

4. In the flowers of *Cypripedium insigne* (Pl. XL, fig. 5), recently seen at Kew, in which the two lateral petals were changed into labella, it is true that the normally fertile stamens a^1 and a^2 of the inner whorl were absent. But this does not prove that they have entered into the construction of the extra lips. It is probably simply a case of correlative development: the extra lip-formation involving economization of material in other, closely contiguous, parts of the flower, and this has meant suppression of the two stamens. Besides, on the Brownian and Darwinian theory for the formation of each lip two stamens are required, whereas there is only one stamen available for fusion with each petal in the proper position. To suppose that each of these stamens has become divided into two for the purpose is an assumption for which there is no evidence whatsoever.

Points against the theory.—The facts and arguments which decidedly seem to tend towards disprov-

ing the accepted theory and to support that advanced by Crüger, are the following:

1. There is no more *à priori* necessity for regarding the labellum of orchids as a compound structure than there is for holding the same view with regard to a perianth-leaf of complex organization in any other plant, *e. g.* the outer perianth-leaves of *Iris*, the nectary-petals of *Aquilegia*, or the posterior sepal in *Delphinium* or *Aconitum*. No special hypothesis is required to explain the presence and structure of the labellum.

2. Wydler found in the bird's-nest orchid (*Neottia*) that the stamens A^2 and A^3 were present, and incompletely fused with the column, yet "the perianth was quite unchanged and retained its irregularity." This fact shows that the labellum can be produced without the intervention of stamens A^2 and A^3 .

3. Hansen described in the 'Gardeners' Chronicle,' and Masters and Penzig describe the same thing, a flower of *Phajus grandifolius* and one of *Odontoglossum crispum* possessing three labella; the stamens A^2 and A^3 not only being present and entirely distinct from the labellum, but being themselves transformed into labella.

The flowers of two varieties of *Dendrobium nobile* have been described above in which three labella were present, the "column" being normal.

Cases like these are sufficient to entirely dispose of the hypothesis of Brown and Darwin; the facts indeed speak for themselves. It might be supposed, possibly, by some enthusiasts for the orthodox view, that the normal labellum, in the absence of the help of its usual lieutenants A^2 and A^3 , had obtained, for its development, that of a^3 of the inner whorl, while the two extra labella had similarly arisen through the timely resurrection of a^1 and a^2 . But apart from the fact that a labellum, on the accepted theory, requires two stamens for its adequate formation, this forlorn-hope-position is at once destroyed by the facts observed

by Masters in a flower of *Cypripedium Sedeni*, which contained two fertile median stamens, A^1 and a^3 , while the remaining four were all in the form of labella. Here there is no increase of members, for all stamens are accounted for in one way or another, and there remain over no possible agencies by which the normal or the abnormal labella could be formed along orthodox lines.

4. Developmental data, as Pfitzer points out, are against the ordinary view. Payer, in studying the flower of *Calanthe*, as typical of the rest of the order, found that the stamens A^2 and A^3 of the outer whorl developed quite separately from the labellum, which is

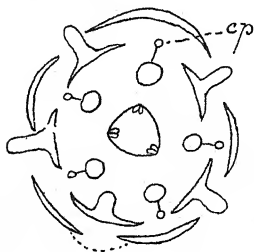


FIG. 120.—*Viola tricolor* (Pansy). Peloric flower, with all petals spurred. Diagram. cp, whorl of carpels attached to stamens.

typically organized while these two stamens can be observed as distinct structures.

Spur-pelory.—Hemsley describes this feature in the lateral petals of all the flowers of an inflorescence of the butterfly-orchis (*Platanthera chlorantha*): a very rare case.

In other cases that half of each lateral petal which is nearest the labellum becomes labelliform, the other half being unchanged.

Mr. Weathers sent a sketch he made of *Angræcum sesquipedale* with a spurred lateral petal, a unique case for this genus.*

In the pansy (*Viola tricolor*), besides the normally-

* Recorded in 'Proceedings of Scientific Committee R. Hort. Soc.,' 23rd April, 1892.

spurred anterior petal, the four remaining ones also bore spurs, thus giving rise to a peloric flower. Owing to the fact that the two lateral anterior sepals were fused together, the spur of the anterior petal was turned inside out (fig. 120).

The best-known cases of pelory are those of the toadflax (*Linaria vulgaris*) and the snapdragon (*Antirrhinum majus*); in these, besides the normally-spurred

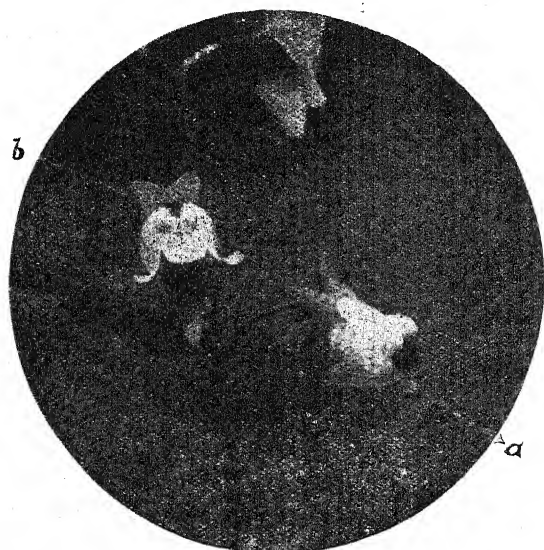


FIG. 121.—*Linaria vulgaris* (Toadflax). *a*, peloric flower with all petals spurred; *b*, normal flower. (E. J. Salisbury photo.)

anterior petal, all the others are also spurred, at least in the completely peloric flowers (fig. 121). Frequently all the flowers of the inflorescence are peloric; this fact, combined with the totally different appearance, as compared with the normal, which peloric flowers present, led Linnæus, Adanson, and Jussieu to suppose that the peloric form of *Linaria vulgaris* was a cross between this and some other species. Sometimes the terminal flower only is peloric.

In *Calceolaria* pelory is not at all uncommon.

Schauer and Moquin-Tandon observed in *Aconitum Stoerkeanum* that all the petals (in the normal flower very small, flat structures) were provided with spur-nectaries, this being evidently correlated with the complete absence of a spur in the calyx. The normal flower of the columbine (*Aquilegia*) may be compared with these cases of spur-pelory.

Spurless Pelory.—As the increase of spurred petals constitutes one type of pelory, so the loss of the spurs in the one or more petals which possess them constitutes a second type, just as we saw also occurred with the calyx.

This type has been seen in the violet (Pl. XLII, fig. 4), and in *Linaria vulgaris*. In orchids the labellum sometimes becomes replaced by a petal in all respects resembling the lateral petals. In *Gymnadenia* and the marsh-orchis (*Orchis latifolia*), however, the labellum, although losing its spur, has become different in form from the other petals. The peloric condition in abnormal orchid-flowers, in which all the petals are alike, producing a "regular" corolla, is, of course, a reversion to the primitive condition which actually occurs normally in the most ancestral group of all, viz., the Apostasiæ, in which *Apostasia* has a perfectly regular perianth and *Neuwiedia* a sub-regular one.

In *Delphinium* the two posterior petals, which are normally spurred, with their spurs inserted in that of the posterior sepal, completely lose them in peloric flowers.

Miscellaneous Pellory.—Leaving the spurred flowers, we come to another type of zygomorphic flower in which there is a greater amount of differentiation among the petals, as in the group Papilionaceæ of the Leguminosæ, where three kinds occur in each flower, viz., the "standard," "wings," and "keel." In such a flower pelory or actinomorphy may arise in two ways: (1) the "wing"- and "keel"-petals become developed exactly like the "standard," giving rise to

"vexillar-pelory," as has been seen in *Lupinus polyphyllus*, *Cytisus Laburnum*, *Trifolium repens*, and *Clitoria*; (2) the "standard" and "keel"-petals become developed like the "wings," giving rise to "alar-pelory," as in *Genista genuensis*. In these peloric flowers it was noticed that all the stamens were free.

In the Labiatæ three forms of pelory have been observed. Peyritsch has paid special attention to the matter in this order. He found that the peloric flowers were nearly always terminal to the main axis of the whole inflorescence, rarely lateral (Pl. XLII, fig. 5); and the sepals of such flowers often leafy and four in number, decussating with the two uppermost pairs of foliage-leaves. Occasionally the peloric flower was the terminal one of a half-verticillaster. In most cases all the petals resembled the lateral petals of the lower lip. In rarer cases, *e.g.* in the lesser calamint (*Calamintha Nepeta*) they all resembled the middle lobe of the lower lip, very rarely the petals of the upper lip.

Peyritsch also observed in *Salvia Pitcheri* and the wild sage (*S. pratensis*) terminal bisymmetric peloric flowers in which two opposite petals resembled the lateral lobes of the lower lip of the normal flower, whilst the two others resembled the middle lobe of the lower lip. Such flowers Penzig terms "hemipeloric."

In terminal peloric flowers of *Streptocarpus* (Gesneraceæ) the dark-purple coloration of the three anterior petals has occurred also in the two posterior ones.

The most commonly cultivated and most striking form of the "Gloxinia" (*Sinningia speciosa*) is that in which the flower is erect and peloric, instead of having the position and shape of all other normal flowers of the same order (Gesneraceæ).

In the Compositæ we frequently find the occurrence of pelory in the corolla of the normally ligulate ray-florets which then become not only actinomorphic, but

greatly reduced in development, and more or less yellow or greenish, as in a variety of the feverfew (*Pyrethrum Parthenium* var. *discoideum*), and of the ox-eye daisy (*Chrysanthemum Leucanthemum* var. *discoideum*); in this last genus we have an instance of a character appearing as an abnormality in one species which in another species, viz., *C. flosculosum* (*Plagiis virgatus*) is a perfectly normal feature. There are also the varieties *discoidea* of the chamomiles (*Matricaria Chamomilla*, *M. inodora*, and *Anthemis montana*), and of the ragwort (*Senecio Jacobæa*); this last represents a condition which is normal in the common groundsel (*S. vulgaris*). Robbins describes pelory of the 3-lobed corolla of the ray-florets of *Gaillardia aristata* which became tubular and 4-lobed; this case thus exhibited partial dialysis of the ligula: the fifth lobe still remained unindividualized.

General Conclusions on Pelory.—The change from a zygomorphic to an actinomorphic condition it is safe to regard as a reversion, for the former is certainly secondary and not primary. This conclusion applies, however, to the mere change as such. But the particular form which the flower or some of its parts assumes under the change cannot by any means in all, or even most, cases be regarded as partaking in the reversion. Possibly the spurless form of perianth-leaves in certain peloric flowers may be, and probably it is, ancestral, for the spurred perianth-leaf is a secondary structure. This will apply to other cases of simplification of perianth-leaves. On the other hand the acquisition of spurs by the four normally spurless petals in *Linaria* and *Viola* must be regarded as a progressive and not a reversionary phenomenon. The form of the petals in vexillar- and alar-pelory of Leguminous flowers must be envisaged in the same way, as also the "hemi-peloric" flowers of Labiatae, and the regular ray-florets of Compositae.

It may be concluded then, that in the peloric flowers here treated of there is a most evident and interesting

admixture of ancestral and progressive characters. But this is merely what we find in so many other abnormalities.

Vuillemin has recently enunciated, in an ingenious paper, the view that peloric flowers are in all cases due to "gamo-gemnie," *i. e.* the "intimate association of two or several floral rudiments." He ascribes the phenomenon to synanthly which has become so intimate and complete that the final result is, to all appearance, a single flower. He classes all peloric flowers side by side with the case of the large terminal



FIG. 122.—*Begonia*. Zygomorphic corolla in male flowers.
(After Hildebrand.)

"peloric" flower of *Digitalis*.^{*} His attention was concentrated mainly on the genus *Linaria*.

It is, however, difficult to see any evidence for the existence of fusion of two or more flowers as a mode of formation of the majority of peloric flowers.

Zygomorphy.—Vidal and also Hildebrand observed irregular flowers in *Fuchsia* in which, in one case, the anterior petals were enlarged, in the other the upper median petal was very large as compared with the three remaining ones; the petals in each flower formed with the upper sepals a kind of helmet.

Hildebrand also observed in a *Begonia* that the

^{*} For the treatment of this case in the present work, see under "Fasciation."

terminal male flower, in the case of three inflorescences, which normally consists of two inner smaller and two outer larger petals, and is perfectly horizontal, had become vertical in position and quite irregular, consisting of a large, helmet-shaped upper and a smaller spoon-shaped lower petal, which latter was notched at the apex (fig. 122). This case is introduced here as an example of the corolla as a whole changing from the actinomorphic to the zygomorphic condition. There does not, however, appear to be any evidence to show that the individual petals, as in all the instances described in the previous section, have undergone any transformation; the change seems rather due to the fusion of the two petals respectively in each pair: the two smaller lateral and the two larger median.

In the so-called "double" *Chrysanthemum* and *Pyrethrum* the change, which has, of course, no connection with true doubling (transformation of stamens or carpels into petals), is due to the regular tubular corolla of the disk-florets becoming irregular and ligulate like that of the ray-florets. We thus see that such capitula assume under abnormal conditions a character which occurs normally in the tribe Ligulæ-floræ. In some varieties of these two plants the disk-florets, normally small and yellow in colour, may not change to the extent of becoming irregular, but their corolla may simply become much enlarged and white in colour. In those which become ligulate the enlargement of the petals is accompanied by fusion of all five to form the anterior ligula.

In the groundsel (*Senecio vulgaris*) the ray-florets have normally a tubular corolla indistinguishable from that of the disk-florets. Occasionally abnormal capitula have been seen in which the ray-florets develop a ligulate corolla; and this feature is, of course, a normal one in other species, e. g. *S. Jacobæa*.

In certain species of *Viburnum*, e. g. the guelder-rose (*V. Opulus*), the outermost flowers of the corymbose inflorescence are, as compared with the inner flowers,

much enlarged, white-coloured, sterile, and often slightly zygomorphic. The same type of corolla may, in abnormal cases, as in the snowball-tree (*V. Opulus* var. *sterilis*), extend to all the inner flowers, so that the inflorescence is sterile throughout; the flowers composing it are, however, hardly zygomorphic, or only slightly so. This is comparable, so far as the change in the corolla is concerned, to the "doubling" of the *Chrysanthemum*-heads.

Camus* observed, in the already zygomorphic flowers of *Viola odorata*, that this feature was accentuated by the reduction of the two posterior petals to quite small, ligulate organs. Penzig points out the interest of this as lying in the fact that this character of the posterior petals is the normal one in the genera *Anchietea*, *Corynostylis*, and some species of *Ionopsidium* of the same order.

All cases in which either the corolla as a whole, or the individual petal, undergoes a change from the actinomorphic or a simple form, to the zygomorphic or a more complex form, represent a progressive phenomenon.

On the other hand all cases of simplification of the flower, as when the zygomorphic changes into the actinomorphic, as when a perianth-leaf loses its spur or its otherwise highly differentiated shape, must be regarded as reversions.

STAMINODY.—This phenomenon is perhaps not quite so common as one might expect. A good case is that mentioned and figured by De Candolle in the shepherd's-purse (*Capsella Bursa-pastoris*), in which, in place of the usual six, there were ten stamens; the four extra stamens were the outermost, and occupied the place of the absent petals, being due to their transformation (Pl. XLIII, figs. 1 and 2).

Battandier observed in some very closely sown, and therefore etiolated specimens of *Papaver malcræflorum*, that the flowers had only two narrow petals, the

* Camus' paper has not been seen.

two innermost having been transformed into two short thick stamens. This is exactly what has occurred normally in *Bocconia*, but in this plant the outer whorl of petals has become similarly transformed, so that this genus is normally apetalous.

A very interesting case in the foxglove (*Digitalis purpurea*) has lately been described and figured by Miss E. Saunders, and the present writer has also seen specimens from the same source. In some plants all the flowers were devoid of a corolla; in the extreme cases all five petals were changed into stamens,

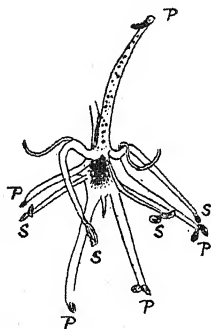


FIG. 123.—*Digitalis purpurea* (Foxglove). Flower showing staminody of petals (*p*). *s*, normal stamens.

so that such flowers were enneandrous; but the most frequent were those in which only the three petals of the lower lip were so changed, yielding heptandrous blooms; also intermediate forms occurred between these two (Pl. XLIII, figs. 3 and 4, and fig. 123 in text).

Eichler observed that the spurred petals in *Aquilegia* had become changed back into stamens. Their normal form is sufficient indication of their erstwhile staminal origin, and this abnormal change in the opposite direction is merely a substantiation of that idea.

Celakovsky observed that in *Ceratocephalus orthoceras* and the mouse-tail (*Myosurus minimus*) 1-3 of the five petals had become changed into stamens,

which were inserted in the $\frac{2}{3}$ cycle proper for the corolla; they were shorter than the other stamens: this also is a case of reversion.

A curious horticultural phenomenon was described by Violle in the rose. A very strong specimen of the "Gloire de Dijon" suddenly produced on all its branches completely "single" flowers; eight days later the usual "double" flowers were formed on the same shoots.

Partial transformation of the petals is not very infrequent. In *Gloxinias* all the petals showed traces of anther-formation in the form of a white stripe running up from the base and terminating half-way up the petal in a small projecting lamina; others bore two rather well-developed anther-loculi in the very middle of the petal.

In some flowers of *Crocus zonatus* the petals were trilobed, and in some of these the middle lobe consisted of an anther.

Henslow describes flowers of the potato in which the petals were almost completely changed into stamens.

In a diseased fuchsia, in which most of the flowers were smaller than in the normal healthy plant, the petals were half-staminate in character, having long stalks and bearing ventral outgrowths. In one case half of the petal was represented by a long-stalked anther.

Partial staminody of the petals is a constant feature in *Amelanchier oblongifolia* var. *micropetala*.

Eichler and F. Müller record that in some abnormal flowers of *Alpinia* (Zingiberaceæ) the petaloid structure (labellum) resulting from union of the two anterior stamens of the inner whorl, became, not only resolved into its original constituents, but these resumed their former character as fertile stamens (see page 84, fig. 95).

In the curious fasciated flower of *Scilla* described on pages 48 and 49, all the petals bore anther-vestigis.

In a peculiar yellow-flowered variety of the potato (a faint lilac and white tinge was also present), which was investigated in Messrs. Sutton's seed-trial grounds at Reading, the petals were all reverting to stamens, their yellow colour being due to this fact; in any given flower one or more petals were connivent towards the centre just like the normal stamens of all Solanaceæ; all five petals had vestiges of marginal pollen-sacs, the ventral ones being absent, but represented by several small ridges or inequalities on the upper surface of the petal.

Streptocarpus has a habit sometimes of developing as enations on the outer surface of the two posterior petals two smaller petals with inverted orientation; occasionally, as in the flowers received from Mr. J. W. Odell, these enations are in the form of stamens,* more or less imperfect, and often showing transitions to petals.

Morphology of the Corona of Narcissus.—An opportunity has recently occurred of confirming the conclusions arrived at by Celakovsky (see *infra*) with regard to the origin of the corona in *Narcissus*; and this in an unexpectedly interesting manner. Two abnormal flowers of *N. Pseudo-narcissus* var. *tridymus* De Graaff were examined† in which the three sepals, the andrœcium, and the pistil were normal. But the three petals were all partially transformed into stamens, and it was owing to this fact that, as it so happened, the nature of the corona became revealed in its true light. In each case the corona of each petal was bilobed, and it was confined to the petals, the sepals being devoid of it; as each petal had its own individual corona it is obvious that the normal corona had become split up. In both flowers the corona of each petal was seen to be an intermediate structure between a petaloid ligular outgrowth from

* A fact which supports the view, set forth above, that such "enations" really represent an extra whorl of floral leaves.

† Obtained from Mr. Chittenden, hon. secretary of the Scientific Committee, R. Hort. Society.

the upper surface of the petal and the basal lobes of the versatile anther; in just the same way as the organ bearing it was an intermediate structure between a petal and an anther. In one petal the corona-lobes were each obviously direct downward extensions, in petaloid form, of the anther-lobes, while at the same time continuous on the outer margin with the normal ligular outgrowth from the petal; and this outer petaloid portion of the corona was a result of the outer petaloid portion of the anther. This was, perhaps,

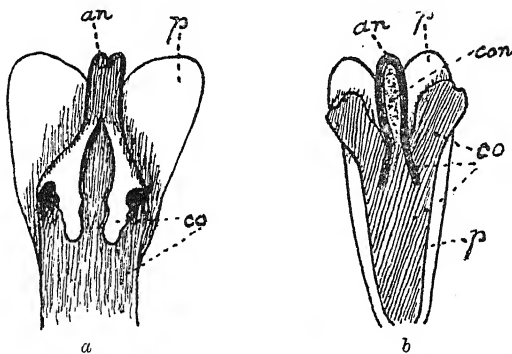


FIG. 124.—*Narcissus Pseudo-narcissus*. *a*, Staminoid petal showing "corona" as a downward prolongation of anther-lobes; *b*, The extreme petaloid portion of "corona" upwardly directed. *p*, petal; *an*, anther; *con*, connective; *co*, corona. Slightly schematized. (From 'New Phytologist'.)

the best case for demonstrating the absolute oneness of the anther-lobes with the corona, the texture and colour of the normal corona being always present. In another petal, besides the downward-pointing narrow anther-lobes having the colour and consistence of a corona, there were two upwardly-directed, broad, petaloid lobes as well, so that in this case the corona was divided into two parts, exactly corresponding to the two parts into which the petal was divided, viz., upper anther-lobes and lateral petaloid portions. In a third petal the basal anther-lobes were partly polleniferous and partly corona-like (fig. 124).

A flower of another variety, sent by the 'Gardeners'

Chronicle,' was also examined, in which each perianth-segment bore a distinct bilobed portion of corona (corresponding to the bilobed basal part of the versatile anther); in the case of one such bilobed individualized portion of the corona, each lobe had on its inner margin an infolded portion, adnate to the upper surface of the corona for some distance below the point of union of the lobes. Such a bilobed corona-segment attached to one of the perianth-segments clearly, therefore, represents a transitional

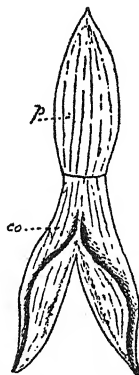


FIG. 125.—*Narcissus Pseudo-narcissus* var. Perianth segment (p) with its bilobed corona-segment (co), showing transition to anther-structure. Semi-diagrammatic. (From 'New Phytologist.')

structure between two basal anther-lobes of the versatile anther, of which the perianth-segment represents the wanting apical part (fig. 125).

The true morphological nature of the corona would seem, from these abnormalities, to be now clearly elucidated.

But the point of chief interest has yet to be mentioned. In the flowers from whose structure Celakovsky deduced his remarkable conclusions it was the petaloid stamens which exhibited the transitional conditions of the corona, and from which he further deduced the staminal origin of the perianth. In the flowers above described it was the staminoid petals

which exhibited the interesting transformations in the corona, which is thus changing back to its original, primitive condition, viz., of basal anther-lobes.

Celakovsky's view of corona-morphology becomes thus doubly supported, viz., by the occurrence of transformations of one and the same organ which are taking place in both directions: progressively and retrogressively.

There is one further point of importance to be noted. In the change which is under way, whereby the three petals become partially transformed into stamens, the entire corona of the flower becomes involved, the sepals being left without any, from which it might be reasonably deduced that in *Narcissus* the normal corona is an outgrowth of the corolla only, and that the sepals, although equally derived from stamens possessing versatile anthers, no longer possess, if they ever did, any structure corresponding to the basal lobes of the anther. The corolla-lobes of other genera of Amaryllidaceæ, although derived by transformation of versatile anthers, are also devoid of any trace of a ligular outgrowth. On the other hand Celakovsky, from a study of abnormal flowers of *N. Tazetta*, found that the calyx possessed a corona as well as the corolla; but that in some of the double flowers, in which the stamens produced corona-structures, that of the calyx was either greatly reduced or entirely suppressed. Hence it would be best, on the whole, to regard the calyx-corona in the flowers of *N. Pseudo-narcissus* var. above described as having also become suppressed owing to the changes undergone by the corolla. In the flower sent by the 'Gardeners' Chronicle,' however, each of the six perianth-segments had its bilobed corona-segment.

In a flower of an *Odontoglossum*, reduced in size from the normal, sent from the Royal Horticultural Society's Gardens at Wisley, the three petals were changed into stamens, although these still remained partly petaloid and the labellum could be distinguished by its yellow

ventral ridges.' The column was normal. What must, doubtless, be regarded as the same phenomenon, although in less accentuated form, is afforded by the extremely rare case of *Odontoglossum crispum* var. "Lady Jane," a "spike" of which Mr. Rolfe received recently from Messrs. Charlesworth's nurseries at Hayward's Heath. All the flowers on the plant are alike in this respect, and the same character reappears year after year. Each of the three petals, including the labellum, possesses a fully-formed, pollinia-bearing anther of two loculi, situated at the apex of the petal; the labellum possesses its usual ventral ridges; the lateral petals have become, quite unlike those of the normal flower, thickly blotched with purple; all three petals are considerably reduced in size. The "column" has remained perfectly normal, hence there is no "wandering" of anthers from this part of the flower into the petals. Everything, therefore, points to the conclusion that this is merely a case (rare though it be, under this form, in orchids) of partial staminody of the petals, hence a reversion; in fact the flowers of this variety are regarded by cultivators as partially peloriate. Magnus observed that in the orchids *Phajus*, *Trichopilia*, *Zygopetalum*, and *Cattleya* the lateral petals were not only changed into stamens, but, like these, were also fused with the "column." Sometimes, as seen in *Zygopetalum*, the labellum does the same thing, and at the same time forms anthers. Sometimes, however, as in *Cattleya Mossiæ*, the petals fused with the column did not form anthers; but the fact that in other cases they do so seems to show the near alliance of these "column"-fused sepals and petals with stamens.

All the above phenomena may be regarded as direct reversions, partial or complete, of the petals to stamens: the organs from which they originally sprang.

CARPELODY.—This is extremely rare; instances are known in the tulip and crocus in which the petals bore marginal ovules. C. Schimper saw petals of the tree-peony (*P. Moutan*) which had on one side the consis-

tence, colour, and hairiness of the carpels, and bore ovules below the stigmatic margin; he also saw ovuliferous corollas in *Rhinanthus* and *Stachys sylvatica*.

Lutz describes flowers of *Crocus sativus* and *græcus* in which stamens, perianth-leaves, and even the bracts bore stigmas.

(3) ANDRŒCIUM.

PHYLLODY.—The stamen, as Masters points out, is so much farther removed in modification from the original leafy ancestor that its backward change into the latter must inevitably be a correspondingly profound one, and less frequently occurring than the same change in sepals and petals. Wolff, Goethe, and Linnæus held that the stamen was of the essential nature of a foliage-leaf, highly-modified structure though it be, and bearing no resemblance whatever thereto.

As will presently be shown, its exact homology with a foliage-leaf can only be demonstrated by means of teratological phenomena. Developmental data are insufficient for this purpose, and moreover wholly misleading.

Celakovsky distinguishes two main types of phyllody in the stamen. Firstly there is the "acrothecal," in which the loculi of each theca remain united at the base and become at an early period leafy in this region, forming a 4-winged bilaminar leaf, while the pollen-bearing portion of the anther occupies the apex of the stamen. Secondly, there is the "basithecal" type, in which the loculi of each theca become separated at an early period, and, especially the marginal ones in the early stages, extend, in an unaltered and pollen-bearing condition, to the base of the anther-blade; on the other hand the anther-blade, in its upper portion, becomes broad and leafy (Pl. XLIII, figs. 5 and 6).

In one plant or another all stages have been seen between the normal 4-locular anther and an ordinary flat green leaf.

THE THEORY OF ANTHER-STRUCTURE.

Morphological Structures of the Upper Surface.

In some of the structural stages, as in those of *Dictamnus* figured by Celakovsky, it is clear that two of the loculi are represented by the leaf-margins, and the other two by laminar outgrowths from the upper surface of the leaf (Pl. XLIII, fig. 7); in more advanced stages of the metamorphosis these laminar outgrowths dwindle in size and eventually disappear. He also has figured, and the present writer has also observed, as described in Vol. I of this work, similar outgrowths from the upper surface of foliage-leaves in *Phlox paniculata* (*decussata*) (Pl. XLIII, figs. 8-10), and they are also found in *Saxifraga ligulata* (Pl. XLI, figs. 5-7) and the lower surface of the leaves of the Indian knot-weed (*Polygonum cuspidatum*).

Celakovsky describes a most interesting abnormal leaf of *Hieracium glanduloso-dentatum* (Pl. XLIII, figs. 11 and 12) which was forked at the apex for a short distance, the inner margins of the two free lobes so-formed being inrolled, and these inrolled margins were continuous with those of two median ventral outgrowths extending from the base of the two lobes to more than half-way down the leaf; this structure he explains as due to dichotomy of the leaf having occurred as far as the extent of the ventral outgrowths and inrolling of the inner margins of the two lobes so-formed, and to a subsequent fusion of the lobes as far as the present base of the fork. At the base of this same *Hieracium*-leaf is a small ventral lobe, with its upper surface directed inwards, which is quite comparable in position to the ventral fertile spike of the *Ophioglossum*-sporophyll. Now he imagines that anther-structure might have been brought about by just such a transformation in the upper half of a leaf as has here been described, coupled with a further dichotomy of the whole leaf so

far as the base where the inner margins so-formed grew out as a pair of leaf-lobes whose inner margins became united with those of the main leaf resulting from its dichotomy, and, at the same time, with the two inrolled margins of its apical portion; the two lobes of the dichotomized main leaf then becoming reunited, a structure would result supplying the two median ventral laminae into which it has been shown that the median anther-loculi may become transformed. The dichotomy, with the exception of

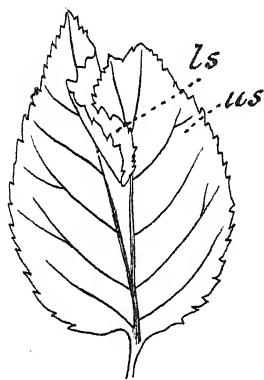


FIG. 126.—*Ulmus* sp. (Elm). Dichotomized foliage-leaf with infolding margins of the apical lobes. *us*, upper surface; *ls*, lower surface. (G. S. Saunders.)

the apical portion, he regards as not externally visible, but as internal.

This may well be the explanation of anther-structure. In a deeply-dichotomized elm-leaf the inner margins of the two lobes tended to become bent inwards; if this were to proceed farther and the surfaces adjoining the margins fused, anther-structure would result (fig. 126). Celakovsky has also described and figured abnormal bracts of the hornbeam showing the same congenital forking and marginal infolding as in the *Hieracium*-leaf, yielding two median lamellæ; in this case they are on the dorsal surface, and the structure is quite unequivocal. While this is a highly probable method

of anther-formation, there are other possible methods to be considered.

For example, and this in itself would cause forking of the leaf, the apex might have become infolded, for a longer or shorter distance,* on to its upper surface, fusion of these two upper surfaces along the midrib subsequently occurring. Such an apical infolding was actually observed in a foliage-leaf of *Saxifraga ligulata* (Pl. XLIII, fig. 13), but in this case there was no fusion of the surfaces. It can be seen that such an infolding, combined with facial fusion, would account for the structure of the upper part of Celakovsky's *Hieracium*-leaf, and would inaugurate incipient dichotomy of the leaf-apex. Another method, which might or might not be combined with that just described, would consist in the fusion of two upturned basal lobes across the upper face of the leaf in such a way that the upper surfaces of the leaf and the basal lobes were opposed, giving rise to such a structure as the basal part of Celakovsky's *Hieracium*-leaf. The basal lobes of a sagittate or hastate leaf might be regarded as resulting from the dichotomy of the basal part of a peltate leaf, or the latter as the result of fusion of two such lobes. If now we imagine the basal part becoming adpressed to and fused by the midrib of its upper surface with that of the leaf along its midrib, the resulting structure would be the two required lamellæ, which might fuse with the two descending from above, and in that way yield us the anther-structure; but the basal lobe might be sufficiently long to fuse with the leaf along its entire length, when no infolding of the apex would be necessitated.† There was observed in *Caltha audicola* an infolding of the leaf-base on either side of the midrib.

* Yet this is, after all, only a variant on the first method.

† Cf. the leaves of *Buddleia Hemsleyana* and *Saxifraga ligulata* described in Vol. I. The structure and interpretation of the *Hieracium*-leaf exactly confirm and agree with the view (arrived at independently) set forth in Vol. I that these "enations" and invaginations, etc., of foliage-leaves really represent stages in the dichotomy of the leaf into two, or in the fusion of two leaves into one. And this view may be applied also to the structure of the anther.

Velenovsky figures a similar instance in *C. biflora*. It was observed that in *C. sagittata* (Pl. XLIV, fig. 1) and *C. dionææfolia* (fig. 127) the leaf possesses two quite free basal lobes which are infolded and adpressed to its upper surface; in the last-named species and in *C. appendiculata* (*C. limbatu*) these lobes were, moreover, completely adnate a third or more of their length to the leaf-surface (Pl. XLIV, fig. 2).

Other species in which such adpressed basal lobes on all the leaves were observed as a normal feature are *C. introloba*, *C. marginata*, and *C. Novæ-Zelandiæ*.* In *Saxifraga ciliata* a medianly-placed, stalked, inversely-



FIG. 127.—*Caltha dionææfolia*. Transverse section of foliage-leaf showing ventral lamellæ, or the upturned basal lobes (*vl*, in illustration of anther-structure. The black part is the upper surface of the leaf. Diagrammatic.

orientated, basal leaflet was seen lying almost flat against the upper surface of the leaf.

The large single basal pocket, or, when this and the main lamina are about equal in development, the pitcher-shaped character of the foliage-leaf (as in *Saxifraga*), of the leafy, or of the petaloid anther, represents merely the stage in anther-formation immediately preceding that in which the median lamellæ are formed; the next step, as shown by so many struc-

* It may be mentioned that in most, if not in all, of these species the apex of the main lamina was conspicuously emarginate, a fact which is of considerable interest for comparison with the forked apex of Celakovsky's abnormal *Hieracium*-leaf. It is suggested, therefore, that in the case of *Caltha* a correlation exists between the presence of median lamellæ (or adpressed basal lobes) and an emarginate apex.

tures, consists of the infolding of the ventral side of the pitcher or pocket and fusion of its median line with the midrib of the dorsal side or main lamina.

Thus, both normally and abnormally, the same structures obtain throughout the vegetable kingdom, a fact strongly in support of the theory propounded in this work on the subject of ventral lamellæ. These facts demonstrate that there is no distinction whatsoever between normal and abnormal structures.

Müller describes an anther of *Jatropha* which was transformed into a trilobed leaf-blade which bore on its upper surface, attached by its midrib, a second rather smaller trilobed leaf, as in *Buddleia* (Pl. XLIV, fig. 3). This structure may be compared with the trilobed* petaloid stamens of the tulip (fig. 129), *Crocus*, etc. This is also comparable to the double vine-leaf described in Vol. I, p. 201, in which the two laminæ were coherent by the upper surfaces of their petioles only (Pl. XLIII, fig. 14). Thus there can be little doubt that the leafy anther of *Jatropha* affords a connecting link between the vine-leaf and the normal anther.

In this anther of *Jatropha*, dichotomy is occurring in the plane of the leaf-surface, as in the vine-leaf. Müller, however, figures another anther of the same plant, representing a scarcely-lobed double leaf in which dichotomy is taking place in a plane at right-angles to the leaf-surface (Pl. XLIV, fig. 4). This leaf may be compared with that of the *Hieracium* described by Celakovsky, when we find that we have before us essentially the same structures.

Thus the modes of anther-formation already suggested, if carried through to the fullest extent, would all equally result in the formation of two distinct leaves, *i. e.* assuming that dichotomy is playing an exclusive part in the structure. Apical or basal invagination, as described above, may equally well, however, be the cause. Fusion of two distinct leaves, as Müller points

* However, the trilobed form assumed by the leafy anther is doubtless due to the fact that the foliage-leaves of this plant are also lobed.

out, is excluded, for a second leaf would not occur in front of the first except in a case like that of our *Buddleia*, where the two opposite leaves of a node become terminal to the shoot; in the *Jatropha*-flower the stamens are lateral structures, so that each stamen can only represent a single leaf. On the other hand, supposing the dichotomy-hypothesis to be true, the forking, in whichever of the two planes it takes place, has never yet resulted in the formation of two distinct leaves. Hence, in whatever way the matter be envisaged, one leaf only is involved in the phenomenon.

Comparison of the Sporophyll of Ophioglossaceæ.

The sporophyll of the Ophioglossaceæ has been probably derived from an ancestral type in which both portions, and not merely the ventral one, were fertile, as seems indicated by the abnormal specimens of *Botrychium* in which sporangia occur on the sterile blade (probably a reversionary phenomenon).

The view is here maintained, as indeed Chrystler has recently clearly shown, that the fertile ventral spike of the adder's-tongue fern (*Ophioglossum*) is the result of the fusion of two lateral fertile leaflets across the upper surface of the sporophyll by their external margins. If now we imagine, as a morphological (even though it may seem far-fetched) possibility, this fertile spike becoming fused along the midrib of its parent-blade, its two parallel rows of sporangia becoming changed, by the solution of the septa, into two elongated sporangial sacs, while similar sacs occurred on the margins of the main blade, the typical anther-structure would be attained. But normally (and note the importance of the fact itself) it is only the stalk of the "spike" which has become thus fused. In fact, the two median anther-loculi may be regarded, on one view of the matter, as homologous in their origin with the fertile "spike" of *Ophioglossum*. This view of the matter has been set forth by Celakovsky.

Bearing this theory in mind, and also the view, above set forth, that the ventral lamellæ of the virescent anther and of the abnormal leaves of saxifrage, etc., represent an imperfectly formed separate leaf,* it is interesting to note what a strong resemblance to a distinct and independent foliar organ the fertile "spike" of the Ophioglossaceæ bears.

Morphological Structures of the Lower Surface.

There remains yet to explain, along the morphological lines of anther-formation, those cases in which two foliage-leaves become fused, or separated off, along the midribs of their lower surfaces, as in the mango- and tobacco-leaves previously described, and the occurrence of enations and pockets on the lower surface, as in *Polygonum cuspidatum*, cabbage, *Ficus benghalensis*, etc.† It will now be shown how anther-formation may quite well have arisen from such structures also; this can be understood much better by a reference to the figures than from any description. We have to imagine the four lamellæ, which arise from the dorsal fusion, or separation off, of two leaves, becoming inrolled in pairs to form four loculi with the upper surfaces innermost. By comparing figs. 4 and 5, Pl. XLIV, we can further see that the two loculi formed by the inrolling of the lamellæ of each original leaf (*me* and *ma*, fig. 128) correspond respectively to a median and marginal loculus which are formed, a pair of such on each side, by the

* I. e. when dichotomy or fusion occurs in the plane of the leaf-surface.

† In the aroid *Xanthosoma atrovirens* there has appeared a sport known as *Caladium appendiculatum*‡ in which all the leaves during the plant's lifetime exhibit lamellar enations from the midrib of the lower surface. These may be simple, or may themselves produce similar enations, but, according to André's account, the secondary ones do not obey the law of laminar inversion, as do the primary ones; or, again, there may occur two sets or pairs of lamellæ whose ends may become united to form semi-ascidial structures, the morphologically upper surface of each being innermost. Here then we see transitional structures between ascidia and ventral lamellæ which tends to support the view that the meaning of both is the same.

‡ Herbarium specimens of this sport were seen at Kew.

inrolling of lamellæ of a leaf fused to another, or separating off, by its upper surface (as in fig. 4). We thus see how the same anther-structure might be produced by two quite different types of leaf-division (or fusion), such as are shown in figs. 4 and 5.

Hence, in a case like that of fig. 5, the surfaces of the two fused leaves (Pl. XLIV, fig. 5) are of necessity in a plane at right angles to the morphologically upper surface of the anther. An anther formed in this way would have its marginal loculi situated apparently on the dorsal side; and such anthers, known as "extrorse," are quite frequent in Nature; in extreme cases the median loculi are also frequently situated more on the dorsal than the ventral side; such conditions are merely due to great convexity of growth on the upper side of the connective. If a similar convexity of growth were to occur on the dorsal side of an extrorse anther which has arisen from the fusion (or separating off) of two laminæ by their dorsal surfaces, then the ordinary introrse anther-structure would result.

In one of the leafy anthers of *Jatropha*, viz., that shown in Pl. XLIV, fig. 4, we see a structure like that in fig. 3, which is brought about by the very intimate fusion of two leaves by their upper (ventral) surfaces forming a single structure. This has dichotomized, and the resultant structure, had we no other clue to its origin, might well be interpreted as the result of fusion of two leaves by their dorsal surfaces, as in fig. 5, and if these became changed into fertile anthers the structure as shown in fig. 128 (p. 170) would result.

From all of which we see that the two kinds of facial leaf-fusion or -fission above described may have given rise respectively to introrse and to extrorse anther-structure, and these two types of anther, however different they may appear from a study of their ontogenetic development, are yet essentially the same.

The enations which sometimes occur, as in the *Polygonum*, along the lateral veins as well as along the

midrib, whether on the upper or the lower surface, may be ascribed to fusion with, or separation from, these veins of lateral lobes of the basal infolded part of the leaf, or also to dichotomy or apical infolding (see above); but these lateral lamellæ can have had nothing to do with modern anther-structure. They are related to, and the result of, the great laminar extent of surface obtaining in the foliage-leaf as compared with that in the anther, hence the lamellæ of the midrib naturally tend to be repeated along the strong lateral veins. The same kind of structure has been seen, though here in the form of detached, almost

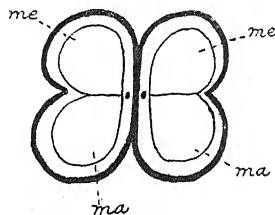


Fig. 128.—Transverse section of extrorse anther taken at the dotted line in Pl. XLIV, figs. 4 and 5, and supposing these leaves transformed into anthers. *ma*, marginal; *me*, median loculi. (Diagram.)

saucer-shaped formations, on the lateral veins of the lower side of the leaf of *Ficus glomerata*.

Nor can we compare directly with anther-structure the basal pocket or pockets occurring on the dorsal side of the *Polygonum*-leaves, but they may be regarded as stereotyped stages in the formation of extrorse anthers; such pockets are a natural result of the presence of two basal infolded leaf-lobes in that position; and it is highly important to note that these basal lobes correspond to the basal extension in a versatile anther.

One may here emphasize the importance of theoretical deduction when based on the proper arrangement of facts for the solution of such a problem as that of anther-structure.

Older Views on Anther-Structure.

The abnormal metamorphoses of the anther show unequivocally that the view held by Cassini and Röper, as also by Neumann and Engler, that the loculi represent merely cavities in the leaf-parenchyma, a view founded on the ontogeny, is a mistaken one. The same may be said of Sachs' view that the loculi represent appendages of the real leaf which consists of filament and connective only; the loculi therefore being regarded as emergences from the leaf.

Velenovsky offers no explanation of the laminar outgrowths from the surface of the leafy anther, apparently not seeing that these need accounting for. He disagrees with Celakovsky's view.

Von Mohl has long ago refuted the view enunciated by Agardh and Endlicher that the stamen is a branch bearing two opposite leaves.

Further Examples of Phyllody.

In the dissociated andrœcium observed by Wydler in *Dielytra*, described on an earlier page, all six stamens were changed into green leaves, the two of the outer whorl into entire, the four of the inner whorl each into half-leaves corresponding with the monothecal character of their anthers.

The stamen of Coniferæ has occasionally been known to proliferate into a leaf, as in the *Araucaria* mentioned by Eichler.

There can be no doubt that the leafy stamen is a reversion in the more distant sense; and the various types of abnormal foliage-leaves cited above show us plainly how its formation has come about.

SEPALODY.—This is well seen in double flowers of certain Ranunculaceæ which are either normally devoid of petals or possess them in the form of staminodes or nectaries and in which the calyx is petaloid. In love-in-a-mist (*Nigella*), columbine (*Aqui-*

legia), and the globe-flower (*Trollius*), doubling is caused by transformation of stamens and the petal-representatives into sepals; in *Aquilegia* this only applies to the variety *stellata*. Braun observed the same thing in *Delphinium orientale*.

Sepalody of the stamen is a progressive phenomenon; the normal sepals, in the plants named above, arose from a transformation of the outermost stamens; the extra sepals are formed in the same way from the remaining stamens.

PETALODY.—Probably by far the best-known of all plant-abnormalities, occurring as it does so universally in most natural orders, and usually as a result of cultivation. "Doubling" of flowers is largely, though not exclusively, caused by this phenomenon. It is to this that we mainly owe the exquisite scent and luscious splendour of coloration in such flowers as the garden rose.

While it is true that, as so many metamorphosed stamens show, the anther is the equivalent of the leaf-blade and the filament of the petiole, the formation of petals, normal or abnormal, may take place in various ways. De Candolle points out that in *Clématis*, doubling, or petalody, is due to expansion of the filament, in *Ranunculus* it arises from dilatation of the anther, in *Helleborus* the petals arise from both filament and anther, and in *Camellia* all three types occur on the same plant. Hence, knowing as we do from the leafy transformations of the stamen that, as a rule, anther corresponds to lamina and filament to petiole, it would be incorrect to conclude that every petal, wheresoever occurring, represents an entire leaf consisting of both petiole and lamina; the morphological nature of any given petal can only be determined from a study of the various transitional stages of the metamorphoses through which it has passed in its evolution from a stamen. Here again we see the great value of the study of abnormal structures. Yet, as showing that all parts of a leaf are really homo-

logous, that, for example, the lamina may merge into the petiole to form a wholly undifferentiated leaf like that of many Monocotyledons, it is known that the 4-laminar or -winged anther-structure may occur, in a semi-petaloid stamen, on the filament and there only, either at its base or throughout its length; or both filament and anther may be similarly con-

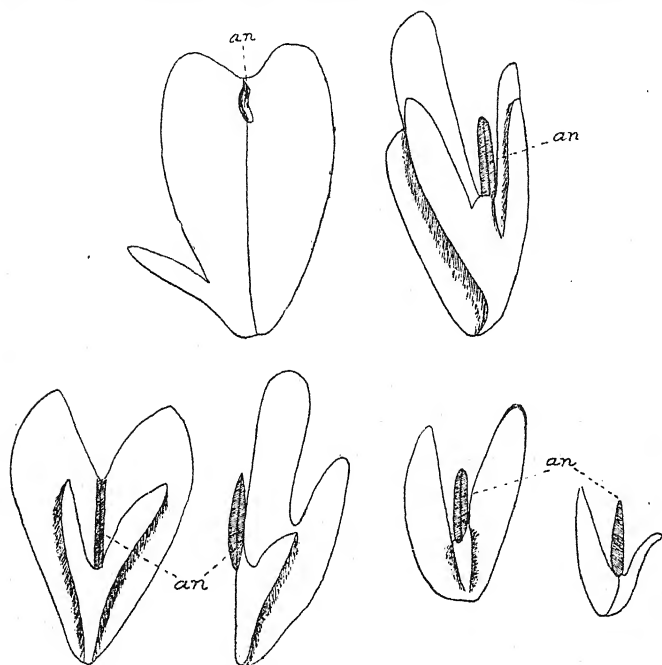


FIG. 129.—*Tulipa Gesneriana* (Garden Tulip). The six stamens of a flower which have all become partially petaloid.

structed in this way. Each wing corresponds to an anther-loculus, much the same retrogressive changes occurring in petaloid as in leafy stamens. Sometimes, however, as in *Rhododendron*, the four wings are present while there occur two complete anthers in the central median position; this may be accounted for by assuming that incipient lobing is taking place, and in each lobe, as in the main leaf, anther-formation

tends to appear. In some semi-petaloid stamens of a tulip such lobing was obvious and such secondary formation of (petaloid) anther-loculi could be seen (fig. 129), for an explanation of which the reader may be referred to the paragraphs under "phyllody" (see also the abnormal *Polygonum*-leaf there described). The case, figured by Masters, of a petaloid stamen of a violet with four lamellæ on the upper surface, may perhaps be explained as follows: that the two outermost lamellæ correspond to the leaf-margins, and that,

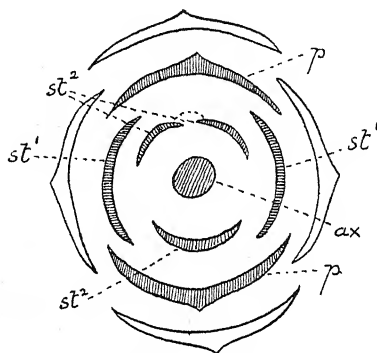


FIG. 130.—*Arabis alpina* (Rock Cress). Diagram of flower showing petaloidy of all stamens, dimerous corolla (p), and proliferation (ax = axis); the two interior stamens of inner whorl (st^2) also fused into one. (After Velenovsky.)

as in the case of some carpels, where the ovules are inserted some little distance away from what appears to be the margin, an extension of the leaf-tissue outwards beyond the real margin has occurred. The ventral lamellæ are homologous in nature with virescent ovules.

In the columbine (*Aquilegia*) there are two kinds of doubling: (1) in which the stamens become changed into petaloid spurred nectaries, and (2) that already mentioned in which stamens and petals become changed into sepal-like structures. Braun observed the same dual type in *Delphinium orientale*, but here none of the petaloid stamens was spurred.

Ritter v. Heufler saw a flower of the toadflax (*Linaria vulgaris*) in which all stamens, including the staminode, were transformed into trumpet-shaped tubes.

Velenovsky observed a remarkable flower of the rock-cress (*Arabis alpina*) in which all the stamens were changed into petals; the pairs of stamens of the inner whorl were represented each by a single petal, so that here fusion, as well as metamorphosis, had occurred (fig. 130).

De Bary observed that, as a result of the attack of the fungus *Peronospora violacea*, the stamens of the scabious (*Knautia arvensis*) were changed into violet petals. Double flowers of the soapwort (*Saponaria officinalis*) are caused by the presence of the smut-fungus (*Ustilago Saponariæ*).

Molliard found that petalody of the stamens in the cowslip (*Primula officinalis*) was caused by the presence of the fungus *Dematium* in the roots; that double-flowered plants of *Saponaria officinalis* were infected in their rhizomes by the fungus *Fusarium*, while single-flowered plants were devoid of it; that petalody in the lesser scabious (*Scabiosa Columbaria*) was due to galls of *Heterodera radicumicola*. He planted normal plants in place of the uprooted anomalous one, and next year its flowers became double, and had fungus on the roots. He states that the association of parasite and host would tend to be accentuated most in cultivation.

Many of the Laurineæ are apetalous, and, as Celakovsky points out, this is due, not to their having lost the corolla by suppression, but because they never had one, as is proved by the fact that the four outer stamens alternate regularly with the 2 + 2-merous perianth as a whole. This view of the matter is strongly supported by Eichler's observation that not infrequently in *Laurus* a corolla is present as a result of transformation of the outer whorl of four stamens. Here, says Celakovsky, is a clear demonstration of how a corolla comes into being.

Rolfe describes double flowers of the orchid *Epidendrum vitellinum* in which there were four whorls of twelve petaloid organs, the two innermost being probably composed of stamens, all those which are normally absent having reappeared; the stigmatic whorl was suppressed.

Masters describes a flower of *Cypripedium* in which the stamens A^1 , a^1 , a^2 had the form of ordinary petals, while a^3 was changed into a labellum, lying immediately within the normal one. Heinricher observed an extra lip formed from the stamen a^3 in *C. Calceolus* and *C. Lawrenceanum*.

Special attention may be drawn to the following cases. Penzig mentions having seen in a great number of orchid-genera the transformation of the posterior stamens of the outer whorl (usually absent) into labella, and attributes the labelliform character to their proximity to the normal labellum. But the facts about to be stated do not altogether support this position. Masters mentions a flower of *Cypripedium Sedeni* in which the two median stamens A^1 and a^2 were fertile, while the four remaining ones were transformed into labella (fig. 131). The great importance of these cases is noted in a previous section. The presence of these supernumerary labella goes a long way in confutation of the Brownian and Darwinian theory of labellum-structure.

In some double flowers of the orchid *Miltonia vexillaria* from Baron Schröder's garden which were examined, dialysis of the column had occurred, accompanied by petalody of the stamens and carpels composing it; the result being that on the posterior side of the flower an extra number of labella and on the anterior side an additional number of ordinary petals were formed. Here we see that the type of petal was determined according to whether it appeared in the near neighbourhood of the labellum or of the ordinary petals, Penzig's views being thus borne out by this case.

In *Miltonia* the cause of the extra corolla-members was in part an increase in the number of whorls (*i. e.* positive *dédoublement*).

In *Iris Kämpferi* and *I. Sieboldii*, in which other reversionary changes, as already described, had taken place, one or two of the stamens of the inner whorl (usually absent) had become petaloid or partially so. In abnormal orchid-flowers, as seen in the above-cited instances, some of the stamens, which are normally absent, tend to reappear under a similar guise.

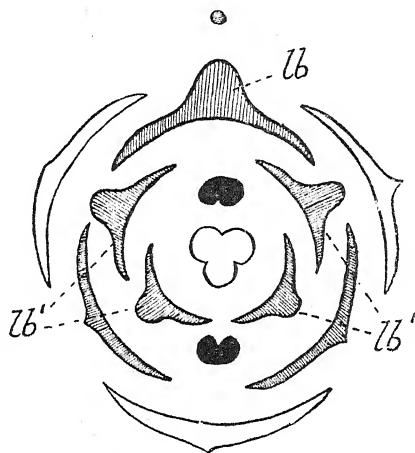


FIG. 131. —*Cyripedium Sedeni*. Diagram of flower showing four super-numerary labella. *lb*, normal labellum; *lb'*, extra labella.

The case of the *Iris* is somewhat exceptional in another way, *viz.*, that when two whorls occur, it is more commonly the stamens of the outer whorl which are the first to become petaloid; and this, of course, is only what should be expected, seeing that they are in proximity to the petals which are themselves petaloid stamens.

Eichler and F. Müller observed in the *Alpinia* mentioned in a previous section, the transformation of the normally fertile posterior stamen of the inner whorl into a labellum, resembling the normal one in the

anterior position (in some of these particular cases, however, represented by two fertile stamens) with the exception of being unnotched at the apex.

Morphology of the "Corona" in Amaryllidaceæ.

Celakovsky observed phenomena of petalody of the stamens in the polyanthus narcissus (*N. Tazetta*) which are of striking importance as throwing a flood of light on the morphology of the *Narcissus*-flower. The salient facts only will be mentioned, referring the reader to the original paper for all the details.

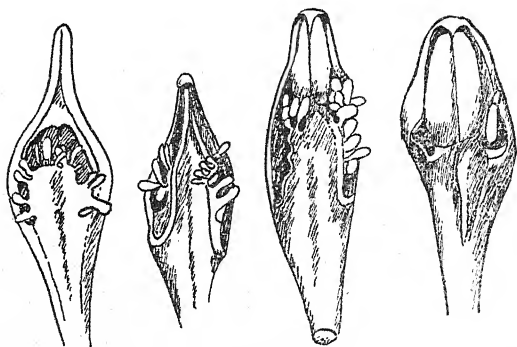


FIG. 132.—*Sempervivum tectorum* (House-leek). Stamens bearing ovules on the ventral lamellæ or upturned basal lobe. (After Von Mohl.)

The normal anther is versatile and the stamen as a whole corresponds to a peltate leaf, or, originally, to a leaf with two projecting basal lobes; supposing transverse expansion of the leaf above the sinus to occur, the two lobes would be carried up into a lateral position; and if, subsequently, they became united by their outer margins across the face of the leaf, a cup-shaped structure would result. In certain double flowers of the above species some of the stamens (the cause of the doubling) had become changed into structures which were clearly imperfectly formed perianth-leaves; in some (and this is the important point) the lamina bore on its ventral surface an outgrowth, either

in the form of two lobes or single, the outer margins of which were continuous with those of the main lamina so as to form a pocket (Pl. XLIV, figs. 6 and 7) or pockets; in other stamens the inner margins of the two excrescence-lobes were continuous with the two median lamellæ of the half-transformed anther (Pl. XLIV, figs. 8 and 9). The ventral excrescence (whatever form it assumed) had always the colour and consistence of the normal perianth-corona. There was also no doubt, from a study of all the numerous structures which these transformed anthers presented, that the ventral excrescence originated from, and was a transformation of, the basal lobes, united or separated, of the versatile anther.* These theories are further supported by the very interesting ovuliferous stamens described by Von Mohl, which are shown in fig. 132. The transitional stages were sufficiently defined to prove this. Moreover, in the case of some stamens, the corona-like excrescence was actually continuous behind the stamen with that of the perianth, this in itself indicating the homology of the two.

The above facts adequately prove that the corona of the normal *Narcissus*-flower, which is a ventral excrescence of the sepals and petals, the originally separate portions of which have become fused, so forming the characteristic tube or trumpet, has been derived from the up-turned basal portion of the anther when that became petaloid.† And it follows further that in this plant both calyx and corolla have been derived from the andrœcium. And we may deduce further from this that in all Monocotyledons in which calyx and corolla are alike in all respects, especially in the Liliacæ, so

* As further proving this he observed in certain double flowers of the daffodil (*Narcissus Pseudo-narcissus*) that the corona of the petaloid stamens appeared in the form of two large lateral lobes, these being in every character corona-like; the outer margins of these lobes are inrolled at the base, and transitional forms between these and a corona-like ventral excrescence were observed (Pl. XLIV, fig. 10).

† See the description in a previous section of the transformation of petals into stamens in *Narcissus*, phenomena which amply confirm the conclusions here reached.

nearly allied as they are to the Amaryllidaceæ, not only has the corolla, but the calyx also, been derived from the andrœcium.

Other Theories of the Corona.

The earlier views as to the nature of the corona of *Narcissus* were as follows. Masters regarded it as composed of the first two whorls of petaloid stamens fused together. Celakovsky comments on this as being the least probable view of all, though never definitely refuted; but certainly never proved. Baillon, relying exclusively on developmental data, regarded it as a cupular outgrowth of the receptacle, of the nature of a disk. But here, as ever, the developmental method is altogether misleading, its followers being ignorant of congenital fusion-phenomena such as this case affords. Döll, W. G. Smith, and Eichler regarded the corona as a ligular outgrowth of the perianth comparable to the corona of Caryophyllaceæ; yet Pax regarded the very similar corona of *Pancratium*, a member of the same order, as composed of the fused stipules of the stamens. As Celakovsky points out, the systematic-comparative, like the developmental method, can throw no real light on the problem. This can only be done by means of a study of the teratological phenomena.

The Abnormal "Corona" and Anther-Structure.

Some light may probably also be thrown on the morphology of anther-structure by a contemplation of some of these structures exhibited by the petaloid stamens of *Narcissus*. In some the corona-like ventral excrescence becomes invaginated towards the upper surface of the lamina, thus reminding us of a similar basal invagination in the saxifrage-leaves above described, and, above all, in the normal leaves of several species of *Caltha*. Also the pocket-shaped forms of stamen (Pl. XLIV, fig. 6; and fig. 132, on left) are exactly equivalent to the similarly-shaped leaves of *Saxifraga*

and *Buddleia*, and to many a petaloid stamen such as one sees, for example, in *Fuchsia*.

As deduced from the structures exhibited by other stamens, this infolding of the ventral excrescence clearly represents the structure which constitutes basal continuation of the outer margins of the lamina with the median ventral lamellæ of such a half-transformed stamen, for in these the lamellæ are continuous with the excrescence lobes.

As Masters points out, petalody of the stamens is more common in polypetalous than in gamopetalous types of flower.

Normal examples of petalody of the stamens occur in Nature, as in the water-lily (*Nymphæa alba*) and *Canna*.

In conclusion, petalody of the stamens must be regarded as always a progressive phenomenon, because it consists in adding a new structure to the original organization of the flower.

HETEROSTAMINODY.—Dunal mentions that in the uppermost flowers of an inflorescence of the mullein (*Verbascum*) the filaments of the stamens were quite glabrous and more or less dilated.

Moquin-Tandon found near Toulouse a plant of the bittersweet (*Solanum Dulcamara*) in which all the flowers had two or three stamens of greater dimensions than the rest; and he points out that this is the normal feature in *S. tridynamum* and *S. Amazonicum*, in which three stamens are larger than the others.

Hildebrand found, in the zygomorphic flower of *Fuchsia* above-described, that, correlatively with the inequality in size of the petals, the filaments of the stamens were of unequal length, precisely as is always normally the case in the zygomorphic flowers of the Labiatæ, etc. In the zygomorphic flowers of *Begonia* observed by him there was no change in the andrœcium.

Conversely, Hildebrand found that in a flower of *Mimulus luteus* all four stamens were of equal length.

Here also we may perhaps place those cases in which staminodes revert to the condition of fertile stamens, as occurs not infrequently in *Pentstemon* and *Scrophularia*.

In the Orchidaceæ Magnus observed in *Dendrobium Wallichii* that the normally fertile stamen A^1 of the outer whorl had become staminodial, while the two lateral staminodes of the inner whorl a^1 , a^2 had become fertile; while J. S. Henslow observed much the same thing in *Platanthera chlorantha*. These cases are interesting, for in *Cypripedium* this structure of the androecium is the normal one.

In *Cypripedium*, where the large staminode, representing the anterior stamen of the outer whorl, becomes fertile, the normally fertile stamens, a^1 and a^2 , of the inner whorl are also sometimes retained. A case like this, abnormal in *Cypripedium*, is the normal feature in *Neuwiedia*, which belongs to the Apostasiæ, a tribe closely allied to the Cypripediæ, both being included in the sub-order Diandræ.

CARPELLODY.—A frequent phenomenon, revealing to us the fact that stamen and carpel are very closely-allied organs, and the facility with which the one may change into the other, doubtless due to the fact that both are derived from a common ancestor, the asexual sporophyll, which exists to-day in some of the more primitive types of plants, such as ferns, horse-tails, and some lycopods. A few instances of this phenomenon will now be cited.

In Hermaphrodite Flowers.

Beginning with those cases in which only a portion of the androecium becomes carpelloid, Roeper mentions a flower of the garden tulip (*Tulipa Gesneriana*) in which there were only twelve floral leaves instead of the usual fifteen, due to the fact that the inner whorl of stamens had been transformed into three carpels which alternated with the three outer stamens, the normal whorl of carpels being suppressed.

In a variety of the common poppy (*Papaver Rhæas*

var. *commutatum*), in many of the flowers some of the stamens nearest the pistil, in one instance more than a dozen, were changed, wholly or partly, into carpels (Pl. XLV), and the upper part of the anther was usually in the form of a stigma. In some of these carpels the margins bear greatly swollen placentas, in others the swollen, hypertrophied placental tissue also extends right across the ventral side; in others, the two ventral loculi of the anther are normal and pollen-bearing, the marginal ones being absent; the ovuliferous placentas occur between the two loculi of each anther-half, *i. e.* some distance from the margin (fig. 133).

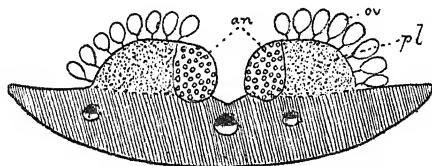


FIG. 133.—*Papaver Rhœas* var. (French Poppy). Transverse section of an anther bearing both pollen-sacs and ovules. (Semi-diagrammatic.) *an*, anther-lobe; *ov*, ovules; *pl*, placenta.

In these cases it is probable that the anther becomes changed into a stigma and the filament into the style.

Sometimes such a carpel is fused with the normal pistil and in that case obeys the usual law in having its upper surface directed outwards; but in one flower all the free carpels exhibited this orientation.*

In the Oriental poppy (*P. orientale*) and the Iceland poppy (*P. nudicaule*) carpelloidy of some of the stamens was also seen.

In the toadflax (*Linaria vulgaris*) flowers were seen in which there were five carpels and in which all the stamens were fused with the carpels, which seems to have been the cause of their becoming carpelloid and having reversed orientation, while they are also placed

* These are facts which again support the views expressed above with regard to the corolla-enations in "*Gloxinia*," etc. In the *free* carpels with reversed orientation in the poppy (which may be regarded as being on the way towards fusion with the normal pistil) we see the converse anomaly to that presented by the extra petals—*fused* with the normal ones, but which yet have normal orientation—in *Datura*.

opposite the carpels: a good case of congenital transposition resulting from the tendency to fuse.*

In the wallflower (*Cheiranthus Cheiri*) all six stamens, in some flowers, while retaining for the most part their normal position, are changed into carpels which are fused with the normal pistil to form a single pistil of eight carpels. The pair of abnormal carpels on each side in the median position are not, in most flowers, united by their margins, and their ventral surfaces are obliquely directed towards the normal pistil, while their replum is excessively deve-

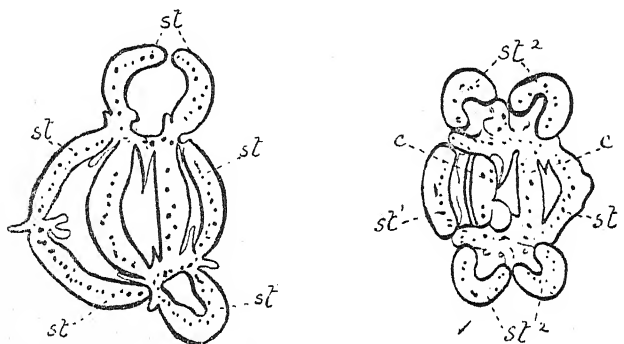


FIG. 134.—*Cheiranthus Cheiri* (Wallflower). Transverse section of stamens and pistil showing carpelldody of the former and their adnation to the latter. st^1 , stamens of outer whorl; st^2 , stamens of inner whorl; c, carpels.

loped and fills all spaces between them and the pistil, helping to cement the whole congeries of carpels together. Each of the transverse abnormal carpels has a replum extending between its margins (fig. 134). In other flowers none of the abnormal carpels are fused either with the pistil or themselves, and each is open, exposing the ovules. In others again an intermediate condition occurs. Usteri saw in hermaphrodite flowers of the papaw (*Carica Papaya*) that the stamens became changed into carpels; when this happened the normal ovary aborted.

* See footnote on p. 183.

Most interesting are the carpellogic stamens described by Masters in the primrose (*Primula vulgaris*); some of these were more or less petaloid, bilobed at the apex and bearing a group of ovules on the midrib of their upper portion; others were much lobed, and, besides the ovules in the position just mentioned, bore also ovules along the margins of the lobes, which were frequently in the form of elongated styles bearing a terminal stigma (Pl. XLVI, fig. 5). Some, again, bore along the midrib, extending from the base two-thirds of the way upward, a placenta-like ridge or swelling bearing ovules on its upper, more swollen part (Pl. XLVI, fig. 6); in some this placenta was very short and bore only two ovules at the top (Pl. XLVI, fig. 7). It is, of course, a very rare, if not unheard of, thing for carpels to bear ovules along their midrib, and this phenomenon of the *Primula* demands explanation. It can be understood by reference to the androgynous stamens of *Sempervivum*, and to the theory of anther-structure given on previous pages, from a consideration of which it can be deduced that this midrib-placenta of *Primula* corresponds to the two median loculi of the anther and to the median lamellæ (ovuliferous in *Sempervivum*, *Papaver Rhæas*, etc.) into which, in abnormal stamens, the median loculi become transformed. But these lamellæ, at any rate, in some types of anther, apparently correspond to the up-turned basal lobes of the leaf fused together by their outer margins, and again fused by the suture so-formed, to the midrib of the leaf. But these fused basal lobes may lose continuity with the margins of the leaf and occur as a ventral excrescence*; Masters describes stamens of *Primula* in which the ventral placenta is detached from the midrib and in the position of a *Narcissus*-corona. The ventral enations on the petals of some of these abnormal flowers must, in this connection, not be forgotten. It is interesting to note that many of the petaloid stamens with

* See *Narcissus*.

median placentas have the forked apex which is a prerequisite for anther-formation according to the first method described when treating of that subject.

The value of these carpellodic petaloid stamens of *Primula* is further shown by the light which, by means of them, we are able to throw on the morphology of the "free central" placentation of this genus. If we imagine these basal, ventral placentas, which are detached from both midrib and margins of the stamen, to become all five fused laterally, the placentas then covering the upward-growing axis in the centre of all, the "free-central" placenta would be attained.

By a comparative study Celakovsky has shown that all carpels without exception are ascidia or pitcher-structures, with a ventral portion formed by the infolding and fusion of the basal margins of the dorsal portion, or of those of lateral segments. He has shown, from Payer's data on the development of the carpels in *Malachium* (Caryophyllaceæ), that in this plant the carpel-margins fuse with each other and with the central axis, the loculi assuming gradually the form of deep pockets; the axis extends some little way above the united carpel-margins; two rows of ovules occur, developing basipetally, along the axis in the neighbourhood of the carpel-margins, and also some little distance above them. On account of their position and basipetal development they are ovules and not independent leaves; hence the whole central axis, not only so far as the upper margins of the carpels, but a short way beyond also, must be clothed with the ventral portion of the carpellary pitcher; and the ventral portion in this case extends at first higher than the dorsal portion. Van Tieghem has shown that the foliar nature of this part of the central axis is also indicated by the reversed orientation of the bundles which belong to the leaf-margins. Celakovsky further points out that we have a right to assume, in those cases where the carpel-margins of a syncarpous ovary do not turn inwards or fuse with the axis, that

the latter is nevertheless clothed with the ventral portions of all the carpels, for, in Primulaceæ, for example, the ovules are developed in the same basipetal manner, and are supplied with inversely-orientated bundles. Hence we must regard the ovary of Primulaceæ, etc., as originally a septate one which has, in the course of time, completely lost all trace of its partitions. Magnus found 2-merous bilocular (below) ovaries of *P. sinensis*, in which no shadow of doubt existed that the ovules belonged to the carpels. So that in the normal carpel of *Primula* the dorsal and ventral portions of the pitcher are alone present, having lost continuity with each other owing to the abortion of the lateral portions; and such a structure is precisely comparable to the carpelloid stamen above-described whose median placenta existed as a free ventral portion of the stamen; also to the perianth-leaf of *Narcissus* with its corona-portion. No doubt, originally, the ovules were situated on the margins of lateral lobes of the carpel. Some of the carpellic stamens show us this original carpellary structure; Masters also figures an open carpel bearing ovules along its margin. As showing the truth of the morphological explanations given above, such carpellic stamens exhibit an extreme reduction of the median ventral placenta, and where separate open carpels occur the placenta sometimes becomes resolved into distinct ovuliferous leaflets, and in other cases the ovules, besides being borne on the margins of the carpels, also occur on their ventral surface.

In the light of these explanations, conjoined with a wide survey over the whole field of both normal and abnormal structures, it is seen how many strange configurations, hitherto utterly inexplicable, become merged together into one single and simple phenomenon, viz., the fusion by their outer margins, across the (usually) ventral surface of the foliar organ, of two basal lobes to form a (usually) ventral lamina, which may or may not unite along its median line

with the midrib of the main lamina; a phenomenon which varies only according to the idiosyncrasy and needs of the organ or organs exhibiting it.

One of the most remarkable of known abnormalities, and at the same time one of the least easy to explain offhand, is the St. Valéry apple; at the place from which the fruit derives its name, a tree, termed variously "Pommier sans fleurs" or "*Pyrus dioica* Willd.," bore flowers all of which had sepals in place of petals and not a single stamen; at a later stage the "fruit" was seen to consist of two "cores," placed one above the

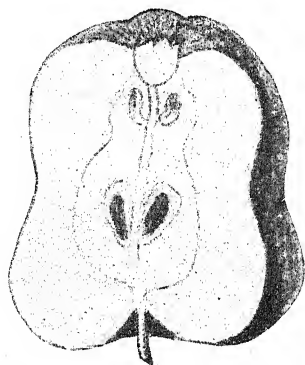


FIG. 135.—*Pyrus Malus* var. (St. Valéry Apple). Carpellody of the stamens. (From Masters, after Tillette.)

other. The appearance is presented of a double-tiered apple having a constriction between the two tiers. At the apex the sepals occur in the ordinary way (fig. 135).

That this structure is due to proliferation of the normal fruit, as some have hinted, seems placed out of court by the fact that in the closely allied species, viz., the pear, when proliferation occurs the normal inferior ovary always completely disappears, and there are never two sets of seed-bearing "cores" as in the St. Valéry apple. It is very unlikely that, if the second tier of carpels were borne on an extension of a central axis, the apple would behave so differently from the pear in this respect. On the other hand the view that

the extra carpels represent transformed stamens is strongly supported by the fact that in the flower the stamens are completely absent; that a lower seed-bearing "core" is always present; and that the number of carpels in the upper tier is often, if not always, twice as many as in the lower. In this fruit the transformed stamens, in the form of carpels, have become intimately adnate to the fleshy sepal-bases; hence the normal sepal-bases have either become further elongated, or, as is more probable, a greater length than usual of each sepal has become involved in the succulent consistence.

Hence, the St. Valéry apple strongly supports the calyx-tube theory of the pome-fruit, and is incompatible with the (at present) more popular axial theory thereof.

The above cases of carpellody are in hermaphrodite flowers. In the poppy the stamens are indefinite in number, and only some of the innermost are transformed into carpels. In the *Linaria*, *Cheiranthus*, and *Primula* the stamens are few in number and all are liable to be changed, thus giving rise to a purely female flower.

In Male Flowers.

We next have instances in which flowers which are normally unisexual, viz. male, become hermaphrodite. This is frequent in *Begonia*. In *B. Cathayana* a male flower bore carpels in the centre, which, to judge by the reduced number of the stamens, had arisen by transformation of some of the innermost of the numerous stamens; in such cases the inferior ovary becomes superior.

Schmitz observed in his abnormal *Euphorbia* that some of the anthers, representing stamens, at the apex of the structures (flower-stalks) axillary to the leafy bracts, became changed into carpels. Immediately beneath this agglomeration of terminal* sessile anthers

* Schmitz, however, held the view that the stamens in *Euphorbia* are of axile nature, and would not, therefore, subscribe to this view of them as terminal foliar organs.

and carpels was the circular swelling normally occurring in the female flower and which some authors regard as a disk, others as a rudimentary calyx (Pl. XLVI, fig. 8). The presence of carpels in this position proves that the anthers topping all these axillary structures which are devoid of any articulation represent entire stamens in which the filaments have become quite suppressed: a very rare case. But it is, in part, comparable to the normal cases on the female side of the Coniferæ, Gnetaceæ, and *Ginkgo* in which the carpel is reduced to an ovule, at least according to the view here held with regard to these structures.

Usteri describes the transformation of male flowers of the papaw (*Carica Papaya*) into hermaphrodite flowers by the change of some of the stamens into carpels; transitions between these two organs were observed.

Again, there is the case of purely male flowers becoming female by the change, not of a portion only, but of the whole androecium into a pistil; this can be seen occasionally in the male catkins of the willow, e.g. in the sallow (*Salix cinerea*), giving rise to an androgynous inflorescence; the two transformed stamens usually become united by their margins to form the bicarpellary pistil of the normal female flower; and it is interesting in this connection to know that in the normal male catkins the stamens frequently become thus united, and this is constantly the case in the variety *monadelphæ*. These facts clearly prove the close alliance which exists between stamens and carpels.

Numbers of catkins were examined from a male tree* of this species; most of these bore flowers in all of which the two stamens were represented by two quite separate carpels borne on long stalks (Pl. XLVI, fig. 10). One catkin consisted entirely of flowers in which the two carpels were united above, but bore pollen-sacs on the inner side of the gaping base

* Kindly sent by Mr. W. H. B. Fletcher, of Aldwick Manor, Bognor.

(Pl. XLVI, fig. 9). Other catkins bore normal male flowers in some of which the anthers showed the first stage of transformation into a carpel. In the above cases the anther of the stamen corresponds to the ovuliferous portion of the carpel, and the filament to its stalk.

From the same source branches of *S. alba* var. *vitellina* were received bearing catkins all of which bore male and female flowers (for the most part of normal appearance) mingled together throughout. Here and there, however, transitional structures were found between stamens and carpels. Pl. XLVI, fig. 11, shows a flower in which one stamen is normal save for bearing a stigma at the apex of the connective, while the other has become completely changed into a carpel. In the case of the female flowers of normal appearance, the transformation had been quite complete; and no flowers could be found in which the carpels were incompletely united.

In the maize the male inflorescences sometimes produce scattered female flowers here and there, evidently replacing the male flowers. Usually the female spikelets occur in the basal region of the male inflorescence. Other cases are known in which the male inflorescence, while completely preserving its usual paniculate form, had entirely changed its sex, producing female flowers only (Pl. XLVII, figs. 6-9). Such a plant would be purely female.

The terminal spike of the sedge (*Carex*) has often normally male flowers at the top and female flowers below, but abnormally the converse is the case, the female occurring at the top. The hop (*Humulus Lupulus*), which is normally dioecious, occasionally bears female catkins at the apex of the male inflorescences.

In the Chinese quarter of the Buitenzorg Botanic Garden in Java a coco-nut palm was observed which bore, instead of the few ordinary fruits at the base of the spadix, great numbers of small, crowded, narrow (quite banana-like) fruits, which created wonderment until it was found that the phenomenon was due to the

transformation of many or all of the male flowers into female. This was described by J. J. Smith.

In such cases as those of the last four plants cited, the change involved is obviously a more profound one than the mere transformation of the stamens of a male flower into carpels; it may be said rather to consist in the congenital transformation of an entire male into a female flower, or of a portion of, or an entire male inflorescence into a female inflorescence, the intervening stages between the two not appearing at all.

Finally, there are those interesting cases where the stamen itself is androgynous, and becomes thereby a bisexual sporophyll. In *Pinus* and *Larix* the stamens are sometimes seen to bear ovules, but this is rare. *Sempervivum tectorum*, as first described by Von Mohl, affords an excellent instance of stamens bearing ovules, and the various stages he discovered of the transformation of a stamen into a carpel are also valuable as hinting at the morphological construction of both these organs. From these cases it is seen how a number of ovules correspond to a single loculus, rows of them occurring either along the outer margins or the median lamellæ (fig. 132, p. 178).

It has been shown on an earlier page that the margins of these median lamellæ really represent the inner margins of two lateral basal lobes of the leaf which have become fused, infolded, and connate by their inner surfaces with the midrib, hence it is quite natural to find ovules in such a position.

We have already seen intermediate structures in the carpelloid stamens of the poppy above-cited. In *P. Rhæas* stamens were also seen in which the median loculi were partly polleniferous and partly ovuliferous, numerous ovules being borne on that portion of the loculus which was sterile and solid. In a stamen of a tulip, one anther-half bore the usual loculi, the other half bore ovules on the outer margin (Pl. XLVIII, fig. 1). In double flowers of the marsh marigold

(*Caltha palustris*) the petaloid stamens occasionally bear marginal ovules.

Miss D. G. Scott has described abnormal flowers of the potato in which some of the stamens, with normal anthers, bore ovules on the filament both on the upper (ventral) surface and in an internal cavity of the filament.

Pl. XLVIII, fig. 2, shows an ovuliferous stamen of the field rose (*Rosa arvensis*).

As regards the meaning of the phenomena classed under carpellody, some of them, such as the transformation of the stamens of a hermaphrodite flower into carpels, or the formation of ovuliferous stamens, merely show that male and female sporophylls are homologous structures. The appearance of female flowers in a male inflorescence may be regarded as a reversion, and it shows that plants which are now mon- or dioecious had at one time mixed inflorescences.

The formation of an hermaphrodite flower by transformation of some of the stamens into carpels probably shows that in the past the unisexual flower was derived by the converse process, viz. the change of the carpels into stamens.

On the other hand the formation of an hermaphrodite flower by the independent appearance of a pistil within the stamens, probably shows that in this case the unisexual flower arose originally by abortion of the pistil.

In all such cases it is probable that the organs would be likely to reappear along the same path by which they disappeared.

(4) GYNŒCEUM.

1. PHYLLODY.—Phyllody of the *carpels* is of very frequent occurrence. Different stages thereof may be observed. In some flowers of *Primula* the styles had merely become green, the carpels being otherwise scarcely changed. In the alsike-clover (*Trifolium*

hybridum) the carpel of some flowers had become enlarged, green, and more or less open, otherwise hardly changed. In the Dutch clover (*T. repens*) the carpels in some flowers were foliaceous, but showed differing degrees of development, for in some the leaf so-formed was unifoliolate, in others bi- or trifoliolate (Pl. XLVIII, figs. 4 and 5). This virescence of the carpels in this species is sometimes accompanied by that of the sepals and petals and atrophy of the stamens. Molliard has shown that virescence in this plant is due to the presence in the stem of the larva of an insect, probably of *Hylastinus obscurus*, which forms galleries in the pith and sometimes penetrates to the cortex. In this way the proper circulation of the sap was prevented. Every abnormal plant examined was shown to contain a larva, while none could be found in healthy plants.

In the melilot (*Melilotus arvensis*) the virescent flowers were found to be due to the presence of the larva of (probably) *Apion melilotii* living in the neck and branches of the stem. No larvæ could be found in normal plants.

In the rose the carpels may become foliaceous while not as a rule reaching the development of the foliage-leaves, remaining simple instead of compound, but this nevertheless constitutes a great change from the normal achene; such leafy carpels also become superior in position. In the "green rose" (*Rosa indica* var.) and in proliferated and fasciated roses this change can be seen; in proliferated roses the modified carpels often form the lower leaves of the shoot which higher up exhibits transitional forms between them and ordinary foliage-leaves.

In the double flowers of the cherry, where two carpels are present, these often exhibit interesting intermediate stages between carpels and green leaves, the midrib being prolonged into a short style, terminated by an imperfect stigma. In very many normal pistils the original marginal placentation has become

quite obscured. When carpels tend to become enlarged or leafy, the ovules are seen to resume their primitive position on the carpellary margins, often at the same time increasing in number. To give merely one instance, Cramer figures such carpels in the carrot (*Daucus Carota*) (Pl. XLVIII, fig. 3).

The green "eyes" or centres of varieties of *Ranunculus asiaticus*, *Adonis amurensis*, etc., are due to a similar transformation.* The other changes of the pistil which are usually concurrent with phyllody are: dialysis (in syncarpous ovaries), increase in number of the carpels, and displacement† from the "inferior" to the superior position.

Turning now to the changes which take place in *ovules*, we find that in the great majority of cases the ovules, when present on leafy carpels, are situated on the leaf-margins. They may be either normal, or in different stages of transformation into leaflets, *i. e.* divisions of the leaf bearing them. These metamorphosed ovules have been observed and described by various authors, and many and varied views have been set forth as to the conclusions to be drawn from them with regard to the morphology of the ovule.‡ The idea that the ovule is a bud or miniature axis was held by Braun, A. de St. Hilaire, Schleiden, and Penzig. The last-named based his view on the fact that he found in *Scrophularia vernalis* nucelli borne at the apex of elongated structures growing on the placenta. Others, like Magnus, were influenced to hold this view by the fact that in some plants the ovule is normally terminal to the axis of the plant;

* The phenomenon of phyllody is useful as showing us that the carpel, whatever its present form may be, is morphologically, as Goethe and Wolff long since pointed out, of the nature of a foliage-leaf, *i. e.* that it has evolved out of this organ in the past.

† The view is supported here that displacement is only apparent in these cases, and that the phenomenon is due simply to lack of fusion between the sepal-bases and the ovary.

‡ For all details see the present writer's historical sketch in which also the untenability of all other theories except the foliolar is clearly shown.

some, again, by the fact that the ovule is often replaced by a vegetative bud. Others held that the ovule is an organ *sui generis*, e.g. Schmitz, Sachs, Strasburger, Goebel, Eichler, and Bayley Balfour. The foliolar theory of the ovule was held by Brongniart (the founder), Robert Brown, Caspary, Cramer, Prantl, Warming, Celakovsky, and Velenovsky.

An account in brief outline will now be given of some of the changes undergone by ovules as fully described by Celakovsky in numerous papers. He regards the ovule as, in a general way, the homologue of a trilobed leaflet of the carpel, of which the terminal lobe, inrolled towards the upper surface to form a cup-shaped structure enclosing the nucellus (this having the value of a sporangial emergence borne on the upper surface of the lobe) is the equivalent of the inner integument; while the two lateral lobes, fused by their inner margins across the upper surface of the leaflet, represent the outer integument. It is to be noted that, in accordance with the law of laminar inversion, the lower surface of the outer integument contacts the lower surface of the inner integument. The above-outlined general position of the author derives its entire support from the facts revealed by the so-called "monstrosities" of ovules where gradual transitional forms between the normal ovule and the trilobed or simple leaflet have been observed.

In abnormal ovules of the garlic-mustard (*Sisymbrium Alliaria*) it was the inner integument which exhibited the greatest amount of proliferation or leafiness; and another remarkable feature consisted in the preponderating tendency to proliferation of the funicle rather than of the outer integument. So that the ovular leaflet sometimes assumed the form of a leafy structure (the funicle) bearing the inner integument, subtended by the rudimentary sheath of the outer integument, on its lower surface (Pl. XLVIII, fig. 6); or, in some cases, the outer integument may be completely absorbed

in the funicular lamina (Pl. XLVIII, fig. 7). Ovules of a similar type were observed in the radish (*Raphanus sativus*).

In this type of ovule, then, we must add an extra pair of lowermost segments to the above-mentioned trilobed leaflet to represent the funicle; a diagrammatic representation of such a leaflet is shown in Pl. XLVIII, fig. 8. Pl. XLVIII, fig. 9, shows the mode in which the middle pair of segments enwrap the inner integument (formed by infolding and fusion of the uppermost pair around the terminal nucellus), and these segments must be, as the diagram shows, folded on themselves towards their inner surface, so as to ensure that their outer surfaces contact the outer surfaces of both inner integument and funicular lamina.

In *Trifolium repens* it was also the funicle which chiefly proliferated, assuming the form of a bilobed structure at the base of whose sinus sometimes occurred the small sheath of the outer integument (from the upper surface of which the funicular lamina is an outgrowth), enclosing the weakly-developed inner integument either in the form of a cup-shaped organ or as a simple leaflet bearing the nucellus on its upper surface (Pl. XLVIII, figs. 10-12). This is a very important stage, and will be referred to again.

The abnormal ovules of the dame's violet (*Hesperis matronalis*) differed from those of both the last two plants, inasmuch as the leafy structure bearing the inner integument consisted solely of the outer integument, as is shown by its sheathing base and by the fact that the margins of the lamina passed gradually over into this sheath (Pl. XLVIII, fig. 13). Hence Celakovsky terms it the "basal lamina" ("Grundspreite"). It must really represent both funicle and outer integument merged into one.*

In this plant the ovule frequently appears as a simple leaflet bearing the nucellus on its upper surface; this

* Just as most Monocotyledonous foliage-leaves represent leaf-base and lamina merged into one.

leaflet cannot be the outer integument, because formation of the inner integument being always the primary process (ovular development being basipetal), this organ could not arise as an emergence from the outer integument; it must also be situated invariably on its lower surface. The leaflet in question must therefore contain within itself both inner and outer integuments. This particular type resulted from the proliferating tendency setting in at the period when the ovule was nothing but an undifferentiated rudiment, containing within itself the two integuments *in potentiâ*. The integuments, whether the outer or the inner, once laid down as completely sheathing structures, never proliferate as laminae. *Hesperis* is particularly interesting as having exhibited a case of a proliferated outer integument bearing two or more inner integuments, the extra ones occurring on the lateral lobes of the leaflet (Pl. XLVIII, figs. 13 and 14); this case, as Celakovsky has elsewhere pointed out, is of considerable value for the interpretation of the female parts of *Cupressus*.

Celakovsky also describes virescent ovules of *Aquilegia*, and these are not easy to understand. The first stage, in which proliferation sets in rather late, shows the inner integument seated on the upper surface of the "basal lamina," the two lobes of which are bent back and fused together behind, instead of, as in all other cases, in front of the inner integument. As this lamina is to constitute the outer integument, there here occurs an apparent contradiction to the usual law of laminar inversion; but our author finds it to be only apparent, for differentiation into an upper and a lower surface has not yet taken place in the inner integument. In the second stage there is an anatropous cup-shaped structure which, from the mode of development and the various modifications occurring during the metamorphoses, is shown to be the inner integument, with which the outer integument is intimately fused along its whole length; the whole constituting a single un-

divided structure. This plant differs from *Trifolium* and *Sisymbrium Alliaria* in the fact that the lower portion of the leaflet never grows out to form a separate individualized lamina. In the second stage just mentioned, where proliferation sets in early, the outer integument remains stationary, while the inner integument alone proliferates as the apical portion of the entire leaflet. The usual relationship between the outer integument and the ovular leaflet is described as follows: the former is an upgrowth out of the lower surface of the lower portion of the leaflet, after this has become inverted and folded in towards the upper surface. There exists, therefore, no essential difference between the case of *Aquilegia* and that of the other plants mentioned above.

De Candolle, Cramer, and others describe abnormal placentas of *Primula* bearing, in place of ovules, more or less completely formed small foliage-leaves; these, as will be seen later, represent the ventral portion of the carpels. It is quite possible for leaflets to develop into complete leaves.

An excellent analogy for ovular construction is afforded by the peculiar leaves of *Codium variegatum* var. *appendiculatum*, of which Celakovsky has given admirable illustrations. In these the blade is divided into two or three distinct parts, separated by a bare piece of midrib. Taking one typical form, let us see the instructive analogy it exhibits with a leafy ovule. The lowermost portion of the blade represents the outer integument; from its lower side springs the middle bare piece of midrib as a result of the formation of a distinct apex to this lowermost portion due to the fusion of two apical lobes across the upper side of its midrib. The bare midrib ends in a terminal lamina representing the inner integument which has a basal pocket, due to the fusion across the upper face of the midrib of two basal lobes of this lamina. If we now suppose the bare piece of midrib intervening between the two laminæ to become excessively shortened or

eliminated, the result would be that the lower surface of the lowermost lamina would be in contact with the similar surface of the uppermost lamina. The apex of the midrib of this last is prolonged into a short bare portion springing from the upper surface of the lamina near its apex, this position being due to the fact that its two apical lobes have fused behind the midrib; the bare piece of midrib thus springing from the upper surface of the uppermost lamina represents the nucellus of the leafy ovule. In this foliage-leaf of *Codiaeum*, therefore, the arrangement and relationships of the three parts are exactly as they are in the leafy ovule, consisting of outer and inner integuments and nucellus.

Again, in the pitcher-plant (*Nepenthes*) the basal, flat, assimilating portion of the leaf may be compared with the outer integument in these ovules, and the pitcher, whose stalk sometimes springs from its lower surface, is comparable to the inner integument with the upper surface inrolled. Eichler has described almost equally instructive abnormal foliage-leaves in *Michelia*.

Indeed, it is quite frequent for the foliage-leaves of many plants to exhibit the same structure that we meet with in the leafy ovule, viz., a basal part bearing a pitcher-shaped upper portion as an outgrowth from its lower surface, or producing the stages which lead up to this. Celakovsky observed such leaves in the lilac (*Syringa vulgaris*) (Pl. XLIX, fig. 6). They have been seen in *Lonicera conjugal* and *Phlox paniculata* (see Vol. I, under "Enations"); in the latter the upper division of the lamina is in the form of a long, tapering, naked piece of midrib. Celakovsky even observed a petaloid stamen of *Camellia* having precisely this structure: the expanded filament bore on its dorsal surface (directed inwards) a pitcher-shaped upper portion representing the anther, whose outer surface was morphologically the lower (Pl. XLIX, fig. 7).

Attention may further be drawn to the strong

resemblance to virescent ovules of the small marginal ascidia in the foliage-leaf of *Saxifraga crassifolia* observed and figured by Goebel and Massolongo. It is clear that some of the virescent ovules are also ascidia of exactly the same form and position.

Exact homologues both of the metamorphosed ovule and of the unaltered ovule or "ovular leaflet" may be found as normal structures in other departments of the vegetable kingdom. Celakovsky finds such in the apparatus of the female "flower" of the Coniferæ. The Taxaceæ present the instance of the normal ovule along with its two integuments; the remaining groups that of the semi-proliferated ovule, of which the seminiferous scale (or rather one-half thereof, seeing that each scale possesses two ovules) is the vegetatively-developed outer integument bearing the involuted nucellus-producing inner integument on its lower (dorsal) surface. The case of *Cupressus*, in which a single seminiferous scale bears several such inner integuments on its lower surface, finds its counterpart in *Hesperis*, as we have seen; such a structure as this might conceivably arise out of a compound ovular leaflet, the terminal segment of each lobe becoming, as in the simple trilobed leaflet, the inner integument borne on that lobe's lower surface. Descending lower in the scale, precisely the same set of structures (although naturally modified in accordance with the idiosyncrasies of the special group of plants in which they occur) are exhibited as normal stages of development in the sporophylls of the ferns. In *Thyrsopteris* and Hymenophyllaceæ we see the case of the normal or slightly leafy ovule of Angiosperms and of Taxaceæ, in which the receptacle bearing its numerous sporangia (homologue of the nucellus), terminal in position, is ensheathed by the integuments, of which the indusium is the morphological equivalent of the inner, while the outer integument is represented by the laminar extension (when present) of the pinnule-segment on either side of the indusium. If now this structure be compared with the virescent

ovule of *Trifolium repens*,* its similarity to the bilobed funicular lamina enclosing the inner integument is obvious: the two structures are to be regarded as homologous although naturally presenting differing degrees of development of the respective parts. In *Dicksonia* the sorus is also terminal to the leaf-segment, but the indusium is here two-lipped instead of cup-shaped. In *Davallia* and *Microlepia* the first stage in the projection of the sorus on to the lower surface is seen, this being caused by the elongation of the upper side of the indusium, which becomes green and is (in part) an extension of the pinnule-segment (the outer integument). The final stage is seen in *Cystopteris*, where the sorus with the lower lip of the indusium is projected completely on to the lower surface of the pinnule-segment (Pl. XLVIII, fig. 15).

In *Cibotium* and *Oyathea* there is a distinct cup-shaped indusium situated on the lower surface of the segment; in the former this is at first terminal and marginal, becoming subsequently displaced into an inferior position; in the latter it is inferior from the first (Pl. XLIX, fig. 3). In these two cases we have the exact counterpart of an inner integument situated on the lower surface of a "basal lamina" or proliferated outer integument or funicle such as occurs in *Sisymbrium Alliaria* and *Reseda* (Pl. XLIX, fig. 4). Pl. XLIX, fig. 5, shows the same thing in a perianth-leaf of a tulip. Completely foliaceous ovules are shown in Pl. XLIX, fig. 1 (*Aquilegia*), and fig. 2 (*Trifolium*).

The present writer is in complete harmony with Celakovsky's view of the subject. But, owing to our utter ignorance of the nature of the original ancestry of the Angiosperms, it is impossible to know the exact form and structure of the sporophyll and its parts out of which the modern carpel and ovules became differentiated; this more especially concerns the primitive

* With which it is more comparable than with the normal ovule.

position of the nucellus or sporangium, whether terminal or lateral to the segment (pinnule).

In any case the leafy carpel and ovule represent reversionary structures, and the various forms of abnormal foliage-leaves described above are an indication of the method by which the peculiar structure of the normal carpel and ovule has been brought about in the past.

Again, the structure of the carpel of *Cycas* strongly supports the ovular theory as above set forth, for it is clear that the ovule of this plant, from its position, corresponds to a leaf-pinna, and the fact that the Cycadean carpel has been derived from the leafy sporophyll of a Pteridosperm shows (what might indeed be deduced without this extra piece of evidence) that the ovule of *Cycas* is a metamorphosed leaf-segment or pinna.

Thus we see how precisely the same structures as are exhibited by these metamorphosed ovules occur as normal structures in the sporophylls of ferns, and as both normal and abnormal structures in the foliage-leaves of Dicotyledons.

Squamody of Pistil.

In some of the secondary flowers resulting from fasciation of the male flower of *Welwitschia*, the centre, where the vestigial pistil normally occurs, was occupied by great numbers of tiny colourless foliar organs which must probably be placed in the category of scale-leaves; there were transitions between some of these and the stamens.

2. SEPALODY.—This does not often occur. In "double" flowers of those Ranunculaceæ in which a petaloid calyx and no corolla, or a corolla of reduced nature, is present, the carpels are frequently transformed into sepals, as in *Anemone*. Duchartre observed in an annual larkspur (*Delphinium Ajacis*) alternating polymerous whorls of sepals and carpels with numerous transitions between

the two. In proliferated flowers of the rose the carpels of the lowermost of the two flowers so-formed were becoming gradually transformed into sepals to form the calyx of the second flower above; from being small, colourless, infolded, and inferior, they became green, expanded, enlarged, and superior, and were immediately succeeded above by the corolla of the second flower. In a case like this the one flower merges gradually into the other, the whole forming, as it were, one continuous, single flower, so that transitional forms exist between the carpels of the lower and the sepals of the higher.

In the "rogue" roses previously described, in which the flower had split into a number of separate inverted flowers, the carpels of the mother flower became superior, green, and inversely orientated in order to serve, in part, as calyx of the secondary flowers.

A somewhat similar phenomenon to that of the proliferated rose occurred in the foxglove, in which the corolla of the second flower caused by proliferation arose immediately above and within the opened ovary whose component carpels were slightly changed to act as calyx for the newly-formed flower.

In each of these three cases just described we see that the type of metamorphosis is in one way different from any that has hitherto been spoken of, inasmuch as the organ concerned becomes changed into a different one, belonging not to the same, but to another flower, and consequently in a direction the reverse of the normal, viz., from below upwards (from without inwards). In these cases sepalody of the carpel is a reversionary phenomenon inasmuch as the carpel becomes enlarged, virescent, and "superior" in position.

3. PETALODY.—A feature of many flowers in which doubling assumes an extreme form, the carpels as well as the stamens becoming affected. A peach-tree, flowering in July for the second time in Kew Gardens, had double flowers, all of which were proliferated, and many of the outermost carpels were petaloid in part. Also in proliferated flowers of *Arabis albid*a both

stamens and carpels were petaloid. In hermaphrodite flowers of *Begonia Pearcei*, in which the stamens were partially petaloid, some of the carpels were similarly affected; in another *Begonia* many of the ovules were also petaloid. In a double *Narcissus* the three styles were more or less petaloid. In the *Miltonia vexillaria* above-described, in which dialysis of the column had occurred, the stamens and carpels composing it had become petaloid.

Cramer and Masters describe more or less petaloid carpels in *Primula sinensis* and *vulgaris* which bore ovules not only on the margins, but also on their upper surfaces, far from the margin; this may be explained as follows: inasmuch as they have become petaloid these carpels probably also possess latent staminal characters, for petals are but modified stamens; hence these superficial ovules probably indicate the latent presence of a median fertile region such as occurs in the anther, but is here occupied by ovules.

A normal case of a petaloid carpel, or part of it, viz. the style, is afforded by the iris; but the most interesting point about its structure is not the petalody, but the possession of well-developed median lamellæ such as occur in some virescent anthers and in the foliage-leaves described above. These lamellæ in their terminal portion form the upper bifid lip of the curious stigma in this plant. Here, then, is one more foliar organ to be added to the already long list of those exhibiting this (from the morphological view-point) profoundly interesting structure.

4. STAMINODY.—This is a phenomenon which might well be expected to occur, seeing what closely-allied organs stamens and carpels really are, and how frequent is the converse phenomenon of carpellody of the stamen.

Its occurrence in *hermaphrodite* flowers will first be considered.

In some very abnormal flowers of the toadflax (*Linaria vulgaris*), kindly sent in the same year (1908)

both by Dr. Rendle and by Vice-Admiral Chase Parr, in which the pistil had reverted to five carpels, amongst other changes, the styles of the carpels of some of the flowers bore imperfect anthers.

A tulip-flower with a 9-merous pistil ($G6+3$) had the ovary split open on one side, and two of the carpels were transformed into stamens which diverged at a wide angle from the pistil. In another flower, also having the ovary slit open, the free margin of one of

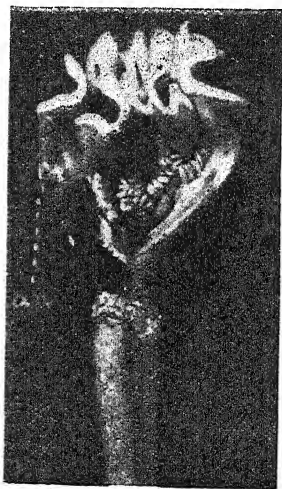


FIG. 136.—*Tulipa Gesneriana* (Garden Tulip). Pistil split open and showing an anther (an) on one of the carpellary margins.

the carpels was transformed into an elongated anther-loculus (fig. 136), while farther to the inside were two free-standing stamens, as if representing an inner whorl of carpels. Both flowers were otherwise normal.

In the fasciated flower of *Scilla nutans*, mentioned in an earlier section, the carpels, which were mostly separate, distinct organs, bore anthers and had no trace of ovules.

The above are cases of hermaphrodite flowers becoming affected; in the tulip and *Scilla* the stamens

become increased in numbers thereby. In some of the flowers of *Linaria* we see a transitional stage to unisexuality, but the carpels are only partially staminoid.

The following are examples of remarkable transformations of ovules. Agardh noticed that in an open ovary of a double hyacinth, side by side with the ovules, anthers were borne on the same placenta. Masters saw and figured in otherwise perfectly normal and closed ovaries of *Bæckeia diosmæfolia* (Myrtaceæ), which in most instances were unilocular, *i. e.* devoid of partition-walls, that ovules were completely absent and replaced by numbers of perfect stamens (occasionally imperfect ones) attached in all cases to the wall of the ovary (Pl. XLIX, fig. 8). We must suppose that here the ovules (segments of a leaf) were congenitally metamorphosed into stamens (entire leaves). The same interpretation may be placed upon Agardh's case. There is nothing really remarkable in a phenomenon of this kind, for a leaflet may exhibit all the characteristics, even as to size and organization, of the entire leaf of which it is a part, hence it would be no more wonderful for an ovule to change into a stamen than into a well-organized leaflet.*

Many instances are known of female flowers becoming male by the transformation of the carpels into stamens, as for example in several species of willow (*Salix*), where usually the two carpels are replaced by two stamens. Wigand saw flowers of *S. pseudo-babylonica* in which the carpels were replaced by three stamens; and transitional organs, partly male and partly female, also occurred in some flowers. Originally, *Salix* must have possessed more than two carpels (an extra number is a frequent abnormality in *Populus*),

* Good examples of this kind of change are afforded by occasional leaflets of the tomato-leaf, which are not only organized exactly as the entire leaf itself, but sometimes produce an axillary bud. Also by the completely organized carpel borne as one of the pinnae of a carpelloid stamen, which was described and figured by Masters.

hence this extra stamen may be regarded as probably representing a third carpel which has become transformed. Zimmermann describes interesting cases of the gradual transformation of carpels into stamens in the crack-willow (*S. fragilis*) (fig. 137).

Plate XLIX, fig. 9, shows a carpel of *Begonia* bearing an anther.

Wigand's observations illustrate the fact that metamorphosis is very frequently accompanied by positive *dédoublement* (an instance has just been cited in *Linaria*), for when the equilibrium of the flower becomes upset, reversion in more than a single respect is likely to occur. In the maize male spikelets sometimes occur in the female inflorescences



FIG. 137.—*Salix fragilis* (Crack-Willow). Carpels changed into stamens. (After Zimmermann.)

or "cobs." They usually appear in the terminal portion of the cob, either as a continuation of the normal rows of spikelets, or on a special prolongation of the axis, as in *Typha*. But they occur more frequently, as might be expected, when the cob becomes resolved into its original separate spikes, and in that case, again, at the ends of the branches; such an androgynous inflorescence comes to resemble the terminal male panicle of the plant. More rarely do the male spikelets occur in the middle region of the cob, mixed up with the female spikelets.

Blaringhem obtained, by artificial mutilation, cobs in which all the female spikelets were replaced by male ones, yet the glumes and paleæ remained the same as in the female flower.

Very interesting are those cases in which the nucellus (megasporangium) of the ovule produces

pollen-grains (microspores). Goebel observed in *Begonia tuberosa* the formation in this position of pollen-mother-cells instead of embryo-sacs (megaspores). Salter observed pollen-bearing nucelli in the passion-flower (*Passiflora*), and Masters the same phenomenon in *Rosa arvensis*.

The same conclusions may be applied here as were drawn from the phenomena of carpellody of the stamen.

Carpellody of the ovule may be the interpretation of a phenomenon described by Masters in which a completely-formed carpel, bearing a long style and a stigma, was borne at the top of an otherwise normal, ovuliferous placenta of *Primula*. It seems to be quite possible for an ovule (*i. e.* a leaflet) to develop into an independent leaf, equal in size and similar in construction to the leaf of which it is a part. A lateral lobe of a leaf has sometimes equalled in development the leaf itself, and this might well become the case in *Primula* where the ovular leaflet is practically separated from its parent carpel.* On the other hand this terminal carpel may merely represent the first and earliest expression of a proliferation of the central axis.

(5) SPOROPHYLLS OF CRYPTOGRAMS.

PHYLLODY.—The sporophylls of the majority of ferns are normally foliaceous; the fertile fronds of many, however, have no green lamina developed, these having probably been reduced from the foliaceous type. The fern-sporophyll most likely represents, in a general way, the type from which those of Gymnosperms and Angiosperms have been derived by a process of simplification.

The completely fertile fronds of certain ferns frequently become partially sterile, thus forming intermediate structures, as in *Osmunda japonica*. In the

* Cf. the fully-formed leaf (*e. g.* in the mango, vine, *Buddleia*) representing the extreme development of the ventral lamellæ which morphologically are the united basal lateral lobes fused with the midrib of the main leaf.

ostrich-fern (*Struthiopteris germanica*), in which the differentiation into fertile and sterile fronds also occurs, Goebel, by cutting off the sterile fronds, induced the sporophylls to exhibit their conformation, but bearing vestigial sporangia.

In the royal fern (*Osmunda regalis*) and *O. cinnamomea* the fertile pinnæ may often become partially foliaceous; in the first-named plant the pinnules of such pinnæ may have one longitudinal half fertile and

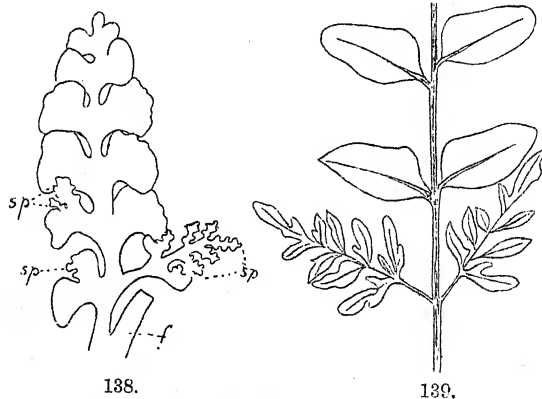


FIG. 138.—*Botrychium Lunaria* (Moonwort). Sterile portion of sporophyll bearing fertile segments. (After Goebel.) *sp.*, sporangia; *f.*, base of fertile "spike."

FIG. 139.—*Aneimia Dregeana*. Basal portion of sporophyll showing sterile lowest pair of pinnæ.

the other sterile, or the upper half may be sterile, while the lower is fertile and contracted to the midrib.

In the moonwort (*Botrychium Lunaria*) the whole of the ventral fertile segment or sporangiophore may become entirely sterile and foliaceous; more frequently only certain pinnæ or portions of such undergo this change.

In *Aneimia Dregeana* the two lowermost fertile bipinnate segments were seen in a perfectly sterile condition in a dried specimen which had been collected by Mr. T. R. Sim near King William's Town, Cape Colony. The sterile segments were not quite so much

dissected as in the normal frond (fig. 139). Mr. L. A. Boodle also observed the same phenomenon in a specimen of *A. hirsuta* which had been sent to England from Jamaica, and whose leaves had been cut off previously; the abnormal leaf had sprouted from the dry rhizome after it was planted at Kew.

In proliferated cones of the horse-tail (*Equisetum*) it is not uncommon to find transitional forms between the peltate sporophylls and the toothed leaf-sheaths. Such were observed in a cone of *E. maximum*; at its base the "collar" had developed as an ordinary leaf-sheath. The abnormal sporophyll, in its least modified stage, had been prolonged on its upper side into a long, tapering scale-leaf structure; one such structure, whose broad peltate base bore three or four sporangia, had three tapering laciniae at the upper end (Pl. XLIX, figs. 10 and 11). In another sporophyll the tapering tip was folded inwards on itself and bore a small sporangium on one of its margins at the base, while the normal large four or five sporangia occurred on the broad, lower peltate part (Pl. XLIX, fig. 12). The most modified sporophylls resembled the ordinary leaves, but in such cases there was a deep downward bend towards the dorsal (lower) side, this bent portion representing the peltate part of the normal sporophyll (Pl. XLIX, fig. 13). A leaf of this kind is a very interesting transitional structure, for it portrays the unfolding and straightening out of the peltate portion of the leaf, which may conceivably have originated in the past by a double fold (downwards and upwards) of the leaf, combined with abortion of the apex. In the last-mentioned case there has been an elongation both in the stalk (to form the sheath) and in the upper apical part to form the tapering sheath-teeth. In one such sporophyll two sporangia were inserted on the dorsal side of the sheath near its edge (Pl. XLIX, figs. 10-13).

The importance of the above abnormalities in *Equisetum* lies in the exact homology which is seen

to exist between peltate sporophyll and vegetative leaf, and in showing the method by which the one type of leaf is able to pass into the other by means of certain modifications of the structure.

SPORANGIODY OF SPOROPHYLL-SEGMENTS.—As an example of the appearance of sporangial tissue on normally sterile portions of the sporophyll, the interesting case of *Botrychium* (Ophioglossaceæ) may be brought forward, in which some of the segments of the vegetative portion become sporangiferous, or even the entire blade (fig. 138). In the former instance this may be regarded as a reversion to the ancient type of fern-sporophyll in which sterile and fertile parts of the frond were more evenly distributed; in the latter we see merely an extreme example, representing an exaggerated swing of the pendulum, which can have no reversionary value.

Poisson mentions and figures an instance of the same phenomenon in the elks-horn fern (*Platycerium biforme*). The rhizome being very short, the fertile fronds, presumably, were unable to develop owing to lack of space. Apparently in compensation thereof, portions of all sterile fronds present, instead of remaining in the normal adpressed and prostrate position, grew upwards and produced sporangia on their upper surfaces.

There may, perhaps, be introduced here a case of androgyny.

Heinricher and Gray describe abnormal sporocarps of *Salvinia natans* (Hydropterideæ) in which both micro- and megasporangia occur. This is obviously a reversion, for in *Azolla* vestigial developments of the one kind are usually found in company with the other, and in Marsiliaceæ it is a normal feature for both kinds of sporangia to occur equally well-developed in the same sporocarp.

General Conclusions.

Already, at the end of each section, generalisations

have been made as to the conclusions to be drawn from each phenomenon described under the heading of Metamorphosis. Partial phyllody of the fertile frond-segments of Ophioglossaceæ and of the fertile fronds of the other ferns may be regarded as reversion to that condition, obtaining in most modern ferns and in the ancient Marattiaceæ, in which fertile and sterile regions of the sporophyll were not so strictly and widely segregated as they are in these forms in which the abnormality occurs. Complete phyllody of the fertile portions, as described in *Botrychium* and *Aneimia*, is merely the extreme swing of the pendulum in the same direction, and has, of course, no reversionary meaning, for the leafy sporophyll, and not the out and out foliage-leaf, was of necessity the original ancestor.

The abnormality in *Equisetum* may possibly stand for a reversion to the character obtaining in the immediate ancestry, viz. in such forms as *Phyllothea*, in which whorls of vegetative leaves alternated with those of sporophylls, a condition found also in the Calamariæ.

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II. SIMPLIFICATION.

As the normal course of evolution has proceeded in the direction of simplication, we might expect what we find to be true, that abnormalities coming under this heading are very much rarer than those occurring under the former one. In fact, all these abnormal structures embody changes which are, for the most part, distinctly in the direction in which evolution appears to be at present tending.

1. ABBREVIATION.

This is the opposite condition of proliferation. Instead of floral or inflorescence-axes being abnormally elongated or present where they do not usually occur, they are abnormally shortened or else completely absent where they usually occur.

1. THE INFLORESCENCE.—In the lady's-smock (*Cardamine pratensis* var. *acaulis*) the internodes of the axis have become suppressed, and the long-stalked flowers arise from the axil of a leaf of the radical rosette. This feature, however, is merely a reproduction of what occurs as the normal character in the genera *Ionopsidium* and *Morisia*, etc.

Wirtgen describes an interesting case of this sort in *Gagea arvensis* in which the flower-scape was entirely suppressed and the flowers arose from the axils of the bulb-scales or from bulbils produced in those axils.

Velenovsky figures a striking example in *Chaerophyllum Tainturiarii* in which the umbels were completely sessile.

There is an abnormal form of the oxlip (*Primula elatior*) in which the flower-umbel is sessile; and another in which the long-stalked flowers arise independently and separately from the leaf-axils; but this may be the result of hybridization with the primrose.

In Umbelliferae, e. g. the caraway (*Carum Carvi*), and the great water-dropwort (*Enanthe crocata*), the secondary umbels are sometimes replaced in part by single flowers; it will be seen that in cases of this sort an attempt is made to reproduce the condition which occurs normally in such forms as *Astrantia* and the sea-holly (*Eryngium*).

2. THE FLOWER.—In some species of *Primula*, by suppression of the flower-stalks, the umbellate is replaced by a capitate inflorescence.

A frequent variation is that in which stalked cones become, like the flowers just mentioned, sessile, as in the club-moss (*Lycopodium clavatum*).

2. ADNATION.

Where floral axes are adnate to another axis, the axillary branch of an inflorescence becomes concre-scent for a longer or shorter distance to the main axis, producing the appearance of an "extra-axillary" shoot.

In the Madonna-lily (*Lilium candidum*) in several shoots a flower-stalk in the axil of a green bract was fused with the main axis as far as the next bract above, opposite which it emerged at the end of a stalk.

A similar case was seen in *Cypripedium* sp.; here the pedicel and ovary of the flower were fused with the axis of the inflorescence above so far as the bract of the following flower which is inserted at the same level as the sepals of the first flower, so that the appearance

is presented of the upper of the two flowers arising from the axil of one of the floral members of the lower one; the inflorescence above the lower flower is represented only by the upper flower and has become almost entirely absorbed by the lower main flower. In *Cypripedium* the upper part of the whole inflorescence is often present and bears two or more flowers; sometimes it is completely absent, having aborted, so



FIG. 140.—*Tulipa Gesneriana* (Garden Tulip). Adhesion of peduncles of two lateral flowers to the peduncle of the main terminal flower. (J. Weathers.)

that the flower spoken of above as the lower one, originally lateral in position and one of a number, comes to be unique and perfectly terminal. This is the same phenomenon as in the vine-stem, in which the stronger lateral axis becomes terminal and pushes the terminal axis into a lateral position; in the *Cypripedium* the extra complication of fusion between the two axes has occurred; this has also been described as occurring in the vine.

Here also may be placed those cases in which tulip-

stems bear more than one flower. Mr. Weathers sent a sketch of this phenomenon in the tulip "*La Belle Alliance*" representing a main scape bearing two lateral ones, of which one is axillary to one of the lower foliage-leaves, the other to an upper foliage-leaf or bract; but in both the peduncles of the extra flowers are adnate to that of the main flower for a longer or shorter distance (fig. 140). Now in *T. biflora* var. *afghanica* the same phenomenon is quite fixed and normal; here there may be as many as seven peduncles, all approximately equal in development and united at various levels; one of these must be the main axis and all the rest axillary shoots, though it is difficult to trace all of the latter to their subtending leaves.

Other normal instances of this phenomenon are frequent. In the borage (*Borago*), for example, the flower-stalk of the terminal flower unites with that of the main inflorescence-axis for a longer or shorter distance. Good examples are afforded by species of *Solanum* and *Crotalaria alata*. Velenovsky ascribes the phenomenon in the two last-named plants to "displacement," as there exists no outward or inward sign of fusion between the two axes; yet in *Loasa papaverifolia*, in which there is an equal absence of any sign of fusion, he states that fusion between the two axes has occurred. The true state of things probably is that the fusion is so deep-seated and radical that no outward or anatomical evidence therefor can any longer be found, whereas those fusions, such as occur in *Lilium candidum*, which are less deep-seated, show clear evidence thereof; it is merely a question of degree. It is difficult to understand how displacement could occur.

Floral axes are sometimes adnate to *foliar* organs. Massalongo describes the occurrence of a group of well-developed flowers on the midrib of the upper surface of leaves of *Amaranthus paniculatus* (Pl. LI, fig. 1), and ascribes the phenomenon to an "enation"; finding no evidence, from the anatomical structure of

the petiole, of any adnation of an axillary inflorescence with the leaf, he declines to accept this explanation. Yet it must surely be regarded as a case of adnation, for adventitious flowers as "enations" from a leaf-surface are entirely unknown. Moreover, the author is mistaken in supposing that the anatomical structure of the petiole can be a reliable guide, one way or the other, in helping to solve such a morphological problem. There are several normal instances of "epiphyllar" flowers, such as those of *Phyllonoma ruscifolia* (Saxifragaceæ) and *Erythrochiton hypophyllum* (Rutaceæ), in which a similar appearance is presented to that of the *Amaranthus*, and in which the adnation is very intimate and complete. It is possible that the union in *Amaranthus* might be so intimate that no trace of it, external or internal, could any longer be found.

Excellent normal examples of the fusion of an inflorescence-axis with its bract are afforded by the lime (*Tilia*) and by *Spathicarpa* (Aroideæ).

We come now to the adnation of floral leaves. Moquin-Tandon cites a case of the adnation of sepals to petals in *Geranium nodosum* in which a petal clave by its lower surface to one of the calyx-segments.

There were cited on a previous page instances, viz. in those flowers where the cyclic tended to become replaced by the acyclic arrangement, of a sepal becoming fused with a petal laterally, so that the double perianth-leaf so constituted belonged partly to the outer and partly to the inner whorl, and was also of dual nature; e. g. in the crocus, tulip, and lily. Buchenau mentions a similar instance in *Tropæolum majus*.

A drawing, kindly lent by the late Mr. G. S. Saunders, showed an interesting case of a flower of *Cypripedium superbiens* (Pl. L, fig. 1) in which the two lateral petals were fused by their margins with the posterior sepal (i. e. the one behind the labellum) to form a single large leaf; the labellum, in correlation with this change, being quite absent (fig. 141). Pl. L, fig. 2,*

* Also lent by Mr. Saunders.

and fig. 142, show a flower of *C. barbatum* in which the petals have united with two anterior sepals (the result of division of the single anterior one). Another drawing showed the same phenomenon in *Disa uniflora*.

Magnus mentions the adherence of sepals to the "column" in various orchids (Pl. LI, fig. 2). The present writer also observed this in a single sepal in two flowers of *Oncidium fuscatum*. Carrière describes and figures in the cherry (*Prunus Cerasus*) a very rare,

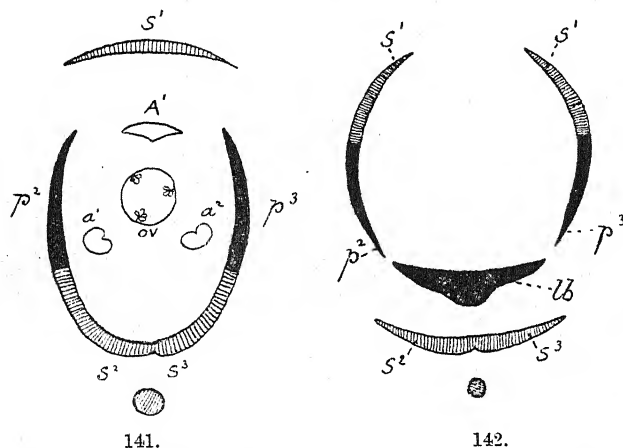


FIG. 141.—*Cypripedium superbiens*. Adhesion of the two lateral petals with the posterior sepal, and suppression of the labellum. Diagram.

FIG. 142.—*Cypripedium barbatum*. Adhesion of the two anterior sepals (arising by division of the single one) with the lateral petals. Diagram of the perianth.

but extremely interesting case in which the sepals, instead of being hypogynous in position, and caducous in duration, were apparently seated at the top of the fruit, and were persistent (Pl. LI, fig. 3, and fig. 143 in text). The interest of this lies in the fact that here we have a character reappearing in one section of the order as an abnormality, which in another section, the Pomeæ, is the normal feature, viz. adhesion (as here interpreted) of the sepal-bases with the pistil to form the so-called "inferior" fruit. This abnormality

affords, therefore, a distinct link, the first one possibly ever seen, between the two sections of the order.

Magnus also cites cases of adherence of petals to the "column" in various orchids (fig. 144).

As regards the adnation of stamens to the petals, Masters writes of this phenomenon: "Morren describes a malformation of *Fuchsia* wherein the petals were so completely adherent to the stamens [outer series] that the former were dragged out of their ordinary position so as to become opposite to the sepals." A *fuchsia*,

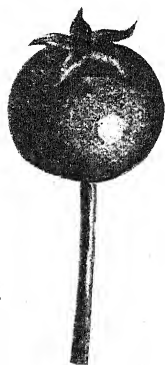


FIG. 143.—*Prunus Cerasus* (Cherry); fruit in form of an "inferior" ovary (after Carrière).

in which a petal, with but half its lamina developed and bearing a complete anther at the apex, had two stamens of the outer whorl completely adnate to it for the whole length of their filaments, the petaloid leaf thus bearing three anthers, one of which, however, was imperfect. Masters observed this adhesion in the orchids *Ophrys aranifera*, *Odontoglossum* sp., etc. In the orchid *Gongora* and some others it is the normal condition. Other normal instances of the adherence of stamens to petals are exceedingly common, *e. g.* in the *Gamopetalæ* and *Narcissus*.

In *Linaria vulgaris*, *Papaver Rhæas*, and *P. orientale*, and in *Cheiranthus Cheiri* adhesion of the stamens (transformed into carpels) with the pistil was observed;

in the two former cases the orientation of the adhering carpelloid stamens was reversed, thereby obeying the law of laminar inversion. Many instances of untransformed stamens fusing with carpels have been seen by other writers. All gynandrous flowers, such as the orchids, exhibit this phenomenon as a normal feature.

In some flowers of the pansy (*Viola tricolor*) which were peloric (all the petals being spurred), there was attached to each stamen at the base, and possessing inversed orientation, a slender style bearing a terminal

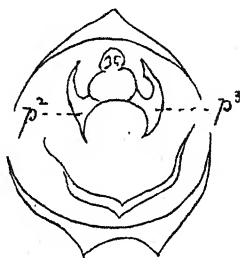


FIG. 144.—*Cattleya Forbesii*. Flower showing the two lateral petals (p^2 and p^3) adherent to the column. (After Magnus.)

stigma, which often bore a minute *Dendryphium*-like fungus. The normal pistil was present. This is a case of the adhesion of carpels to stamens as distinguished from the converse condition just described.

3. COHESION AND SUPPRESSION.*

SYNANTHY.

This is precisely the opposite phenomenon to forking and fasciation of the flower; but the term "synanthly" has been applied in the past, *e.g.* by Masters, to phenomena which should be included under the head of bifurcation or fasciation, it being preferable to hold

* Under this term will be included "abortion," "degeneration," and "suppression," as these are merely different degrees of one and the same change.

these distinct from synanthly as due to the imperfect partition of a single structure. It is often difficult, when confronted with compound flowers, to know whether one is dealing with partition or synanthly. Each case must be decided on its own merits; and synanthly may only be definitely determined where it can be shown that an actual displacement of flowers on the axis has taken place, or where an apparently compound flower is known to be replaced in a normal inflorescence of the same or an allied species by two or more free, separately-organized flowers.

R. R. Gates describes interesting cases of synanthly in the evening-primrose (*Enothera*)*; he states that every polymerous flower has two bracts at its base instead of one; the bracts may be independent or more or less coalesced at the base. The ovary and hypanthium were more or less flattened. "An examination of the stems which bore these polymerous flowers disclosed the fact that they exhibited irregu-

* Some of Dr. Gates' observations on *Enothera* are here appended (K = calyx, C = corolla, S = stamens, N = stigma-lobes).

| | | |
|-------------------------------------|--|--|
| 1. $K_3C_3S_4N_{11}$ | <i>O. multiflora</i> | Two bracts at base of flower. |
| 2. $K_6C_6S_{12}N_8$ | " | Two bracts partly coalesced. |
| 3. $K_6C_6S_{12}N_8$ | " | Two bracts at base. |
| 4. $K_4C_4S_8N_4$ $K_4C_4S_8N_5$ | } Race No. 25 from near Liverpool | Two perfect 4-merous flowers with their hypanthia in contact through- out their length and partly fused. Ovaries in contact, and partly fused. Two bracts. |
| 5. $K_3C_3S_8N_6$ | <i>O. biennis</i> × <i>Lamarck-</i> | One bract. |
| 6. $K_3C_3S_8N_4$ | " [iana | One bract. |
| 7. $K_3C_3S_8N_5$ | " | One bract. |
| 8. $K_6C_6S_{12}N_8$ | <i>O. grandiflora</i> from Alabama. | Hypanthium and ovary flattened. One bract. |
| 9. $K_5C_5S_8N_?$ | Race 54 × 40. | One bract. |
| 10. $K_5C_5S_8N_8$ | <i>O. biennis</i> , Chelsea | Only one bract at base of each flower |
| 11. $K_5C_5S_8N_8$ | Physic Garden. | in this race. In one case the bract had two tips, as though resulting from the incomplete coalescence of two bracts. |
| 12. $K_5C_5S_8N_5$ | | |
| 13. $K_5C_5S_8N_7$ | | |
| 14. $K_5C_5S_8N_5$ | | |
| 15. $K_5C_5S_8N_5$ | | |
| 16. $K_5C_5S_8N_5$ | | |
| 17. $K_5C_5S_8N_5$ | | |
| 18. $K_5C_5S_8N_5$ | | |
| 19. $K_5†C_4S_9N_4$ | | |

† Two sepals of normal width, three narrower, occupying about the width of the other two.

larity in the placing of these flowers on the stem, or in other words variations in phyllotaxy. The flowers and their bracts were not uniformly distributed on the stem, but certain flowers were very close together and others long distances apart." This variation in the phyllotaxy, showing that a flower here and there has been displaced from its usual position and approximated to or fused with another flower, is the only evidence present that the polymery of these flowers is

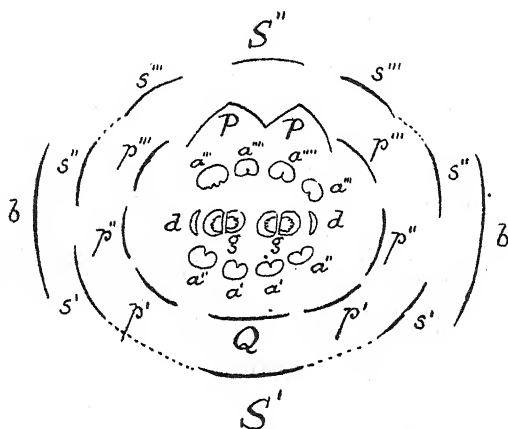


FIG. 145.—*Pedicularis sylvatica* (Red-rattle). Diagram of dual flower due to conrescence of two flowers. *bb*, bracts; *S*, product of fusion of two sepals each from a different flower; *s*, independent sepal; *p*, *p'*, *p'''*, petals of lower lips; *PP*, petals of upper lips; *Q*, petal of doubtful origin; *a*, stamens; *g*, ovaries; *d*, disks. (After Wigand.)

due to synanthly and not to fission, as without such evidence it well might be.

Wigand made an interesting observation in the red-rattle (*Pedicularis sylvatica*): in one plant the two uppermost flowers of the inflorescence were conrescent to form a terminal peloric flower: a rare case (Pl. LI, fig. 6, and figs. 145 and 146 in text).

Fusion between two of the numerous crowded flowers in the verticillaster of Labiatae has been noted: a by no means surprising occurrence.

Costerus and Smith describe a case of fusion of the

two flowers which normally occur side by side in *Canna*: in this dual flower there were 7 sepals, 5 petals, 6 alæ, 2 labella, 1 normal stamen; the petaloid portion of the other stamen is notched and bears a ridge which near the anther ends in a free lobe. There were two styles, one normal, the other filiform. The ovaries were simply united along one side only.

Migliorato described instances of concrescence of flowers in the inflorescence of the gum-tree (*Eucalyptus salicifolia* and *E. viminalis*), etc. (Pl. LI, figs. 4 and 5). In the genus *Syncarpia*, belonging to the same

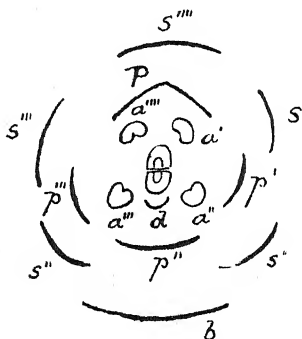


FIG. 146.—*Pedicularis sylvatica* (Lousewort). Diagram of normal separate flower. *b*, bract; *s*, sepals; *P*, upper lip; *p*, petals; *a*, stamens; *δ*, disk. (After Wigand.)

section of the Myrtaceæ, the flowers are normally concrescent, forming a solid mass. In *Eucalyptus cornuta* they form a very compact aggregate, and are in part concrescent, but not completely so. In most species they are completely free.

Synanthly occurs as a normal phenomenon in the genus *Lonicera* (honeysuckle). Arber has investigated this, and to his paper the reader is referred for further details. It is a case of partial synanthly, inasmuch as the ovaries only of the two lateral flowers of the dichasial cyme are united (to form a false berry), the entire upper part of the flowers being free. This we know to be due to union and not division, for, by

comparison with other species of the genus we find the original condition to have been a dichasial cyme of three flowers, of which in some the terminal flower has disappeared, the two lateral ones being still free, in others, as *L. alpigena* and *L. Xylosteum*, the third step has been taken in reduction, viz., union of the two lateral flowers.

Now, it is of great interest to find, as described by Velenovsky, that in *L. Alberti* (in which species flowers with both perfectly free and those with fused ovaries normally occur) abnormal flowers sometimes are found in which the upper portion of each flower, viz. the corolla and andrœcium, become as intimately fused as do the ovaries; such a synanthic flower then possessing a 9-merous corolla and andrœcium (Pl. LI, figs. 7 and 8).

The phenomenon of synanthy is a progressive one.

NEGATIVE DÉDOUBLEMENT.

The term "negative dédoublement" was applied by Celakovsky to all those cases in which at some stage of the development the primordium is double, or shows a tendency towards doubling, but in which the phylogenetic tendency is towards fusion. Suppression represents a further evolutionary step in the reductive direction.

GENERAL.—Those cases are included here in which the flower as a whole is affected by the reduction-process, fusion or suppression or both occurring in all the whorls.

Examples of reduction to *pentamery* will first be mentioned.

In *Lilium candidum* it was noticed that on several plants the terminal flower of the inflorescence was partially 5-merous. The two perianth-whorls, each normally 3-merous, had rearranged their parts so as to make a single 5-merous whorl; of these five leaves, two are completely external and devoid of dorsal

grooves; one is partly external and partly internal with a dorsal groove on its inner half only (these in all probability represent a fusion between a petal and a sepal, causing thereby the 5-merous condition of the flower); two are completely internal, with dorsal grooves on both sides (Pl. LII).

This 2 + 3-merous perianth of *Lilium* may be compared with the normal structure of certain Restiaceæ and Triuridæ, but in this case the condition is due to suppression of an outer leaf, as Celakovsky points out. He also cites a similar normal case to this in the Polygonaceous genus *Podopterus*. The 2 + 3-merous perianth of the knotweed (*Polygonum*) is therefore probably also due to the same cause. But in all these cases the common factor is the derivation of the 2 + 3-merous perianth from an original 3 + 3-merous one, like that in the dock (*Rumex*) and the normal flower of *Lilium*.

We have therefore in these 5-merous perianths, normal and abnormal, a transition between two whorls (an outer of three and an inner of three), in which the third leaf* is partly, so far as insertion is concerned, in the inner and partly in the outer whorl.

These terminal 5-merous flowers of *Lilium* (only flowers in this position showed the feature) are exactly comparable to the 5-merous flowers (in all whorls save the pistil) of the barberry (*Berberis*) in which genus the lateral flowers have a calyx of 3-merous whorls. Eichler points out that this 5-merous calyx of the terminal flower of *Berberis*, as also the 5-merous calyx of most Ranunculaceæ and all other Dicotyledons, may be regarded as derived from, or equivalent to, an outer whorl of two and an inner whorl of three members; this is shown by the fact that often the two outer members are laid down a considerable interval before the three and following members appear. This is regularly and normally the case with the calyx of Cruciferae, and other Rhœadales, some of

* Counting from below.

whose older members, as *Papaver*, are clearly closely allied to, and derived recently from, the Polycarpicæ (as Celakovsky points out), and have their parts in threes.

The corolla of Portulacaceæ is also 2 + 3-merous, its perianth having three whorls in all, like that of the Papaveraceæ and Cruciferæ.

In the lily-flower there were five stamens which did not alternate exactly with the perianth-leaves; the pentamery here was probably due to fusion of two stamens; but this was not particularly noted. Of the normal three carpels two were partly fused together. The formula of this flower was therefore $K2\frac{1}{2} C2\frac{1}{2} A2 + 3$ (or $3 + 2$) $G2 (-3)$. A second terminal flower had just the same structure. A third had a perianth of four leaves, of which one was completely external and one completely internal, and two (lateral) ones which were half external and half internal, representing a fusion of two sepals each with a petal; there were five stamens and three carpels. The floral formula in this case would be $K1\frac{1}{2}\frac{1}{2} C1\frac{1}{2}\frac{1}{2} A3 + 2 G3$. A fourth flower had the same 5-merous perianth, but andrœcium and gynœceum were normal. Pentamerous flowers of *Pancreatium* and *Narcissus Pseudo-narcissus* may also be mentioned.*

Tetramerous flowers replacing the normal 5-merous ones are not infrequent in Dicotyledons, as in examples observed in *Pentas*, *Primula*, and *Passiflora*; in this last flower there were only two carpels.

Trimerous flowers were also exhibited by a *Pentas*. *Fuchsia* offers another case. Magnin describes a plant of herb-Paris (*Paris quadrifolia*) which was 3-merous throughout, thus showing a reduction by one member in all its whorls.

Dimerous flowers, which at the same time naturally become pre-eminently peloric, are common in orchids;

* A 5-merous flower of *Tulipa persica* was recently seen in which two perianth-leaves were completely external, two completely internal, while one was half in- and half outside. There were five stamens alternating with the perianth-leaves, and two carpels.

such were often seen, as in *Grammatophyllum*, *Cypripedium*, *Cattleya*, and *Narcissus biflorus*.

In a flower of *Grammatophyllum* there were two sepals (anterior and posterior), two lateral petals, and two carpels.

In another orchid, *Cypripedium insigne*, the anterior sepal was absent; the posterior sepal, normally consisting of the two fused lateral sepals, was rather deeply split and one half had become displaced a good deal to the right; there were two labella (anterior and

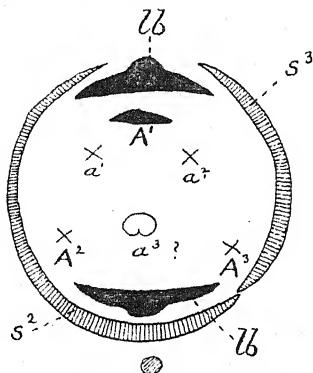


FIG. 147.—*Cypripedium insigne*. Diagram of perianth and androecium. s^2 , s^3 , lateral sepals; lb , labella; A^1 , stamen-like staminode of outer whorl; a^3 , median stamen of inner whorl?

posterior); the two lateral stamens of the inner whorl (normally present) were absent, or else fused to form the single fertile stamen which was present, or else this represented the median stamen of the inner whorl; the staminode was quite stamen-like in appearance, but still barren (fig. 147).

Masters described in the 'Gardeners' Chronicle' an interesting 2-merous flower of *C. Harrisianum*. The calyx was practically normal, consisting of two sepals situated fore and aft; these were, however, exactly similar in every respect. The lateral petals were also practically normal, but were placed sharply at right angles to the plane of the sepals. Of the components of the column there were two large staminodes,

exactly similar to each other, belonging to the outer whorl; the extra one must, therefore, have arisen from fusion of the anterior stamens A^2 and A^3 , after these had become abnormally resurrected in the form of staminodes. Stamens a^2 and a^3 of the inner whorl were normal, but situated exactly at right angles to the staminodes and opposite the petals. The usually

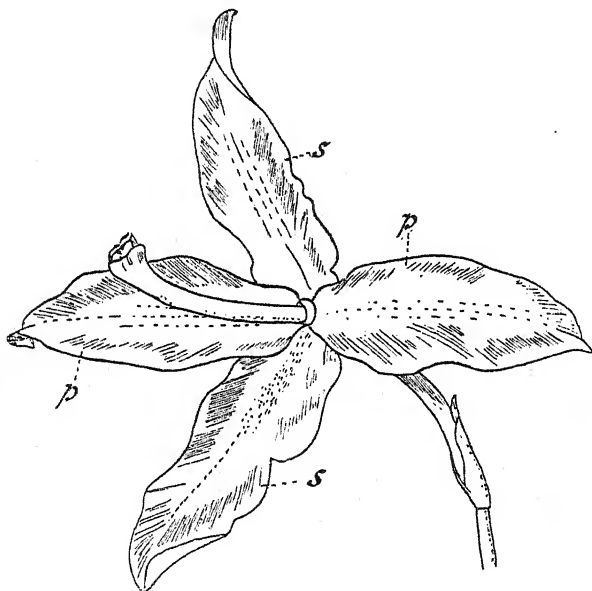


FIG. 148.—*Cælogyne cristata*. Dimerous flower. (From the 'Gardeners' Chronicle,' 1903.) s, sepals; p, petals.

trilobed stigma had become a square one, doubtless representing the two apical stigmas of a bicarpellary pistil alternating with the stamens a^2 and a^3 ; the ovary was single-celled and devoid of ovules. The most interesting feature of this flower was the appearance of an extra staminode in order to complete the symmetry of the flower, this being the only case of "positive dédoublement"; in all other whorls the structure had either remained *in statu quo* or else "negative dédoublement" had occurred.

In a flower of *Cattleya labiata* there were two sepals (anterior and posterior) and two lateral petals; no labellum. Fig. 148 shows a flower of *Calogyne cristata* in the same condition.

In a flower of *C. Loddigesii* var. *Harrisoniæ*, on the other hand, there were two lateral sepals, and two labella (anterior and posterior) (Pl. L, fig. 3).

In *Narcissus biflorus* every alternate whorl was 2-merous (fig. 149).

Wherever pentamery occurs in Monocotyledons we see a trace of this same tendency to reduction in every alternate whorl.

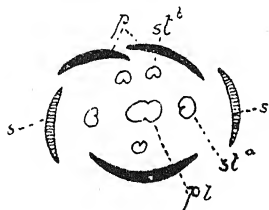


FIG. 149.—*Narcissus biflorus*. Dimery in the calyx, the first whorl of the androecium, and the pistil. s, sepals; p, petals; st^a, first staminal whorl; st^b, second staminal whorl; pl, pistil.

F. Müller describes flowers of *Hedychium* which were 2-merous throughout; the usually bifid labellum was in these flowers quite entire.

Engler describes various interesting flowers of the yellow rocket (*Barbarea vulgaris*) which were 2-merous throughout, the whorls being often so many as seven or ten; often all or most of the transverse whorls had bifid leaves (including a transition to 4-mery), while the median ones had simple leaves. The floral members in these flowers were mostly virescent.

Heinricher* found "incompletely 2-merous (pseudo-dimerous) flowers of *Iris hungarica*, whose perianth was constructed exactly like that of normal flowers of Philodraceæ. The two posterior leaves of the outer

* The original paper has not been seen, so the facts are taken from Celakovsky's account of it, and no excuse is made for quoting at length from this source, the matter being of such importance.

perianth-whorl were united into a double-leaf, recognizable by the two parallel beards; of the inner whorl only the two lateral anterior ones were present. Of the single outer staminal whorl the two posterior stamens were so closely approximated as to form a pair in front of the two beards. Of the two median stigmas the posterior was a two-keeled double-leaf. The ovary was indeed bilocular below, but the two posterior loculi were smaller, opposed to the anterior one, and fused into a single loculus above (fig. 150 *a*).

"In a second flower the 2-merous condition was still more pronounced. Here the two posterior perianth-

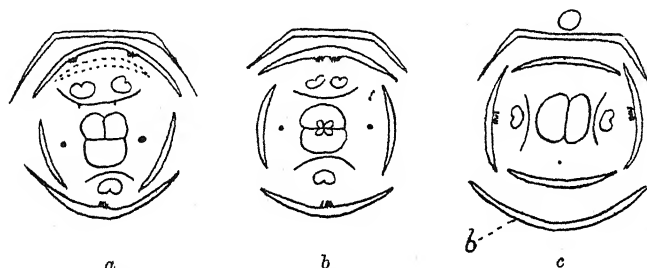


FIG. 150.—*Iris hungarica*. *a*. Diagram of flower showing transition between di- and trimery. *b*. The same; change to dimery more complete. *c*. Diagram of completely dimerous flower of the more usual type. *b*, bract. (After Heinricher.)

leaves were so intimately united that only a single beard, divided at its upper end, was present, and the two leaves of the inner whorl were exactly transverse. Of the staminal whorl only two median members were present, of which the posterior bore a double anther which was bipartite above. The carpellary whorl was completely 2-merous (two stigmas, bilocular) and median. There had thus obtained in the first, third, and fifth whorls a more or less complete union of the posterior members; in the second and fourth whorls, however, suppression of the posterior members (along with displacement), all according to the law of reduction (fig. 150 *b*). The only really remarkable point to notice is that the first perianth-whorl, which has

become 2-merous, is placed medianly, instead of, as Heinricher (and also Eichler) found in other completely 2-merous flowers (fig. 150 c), alternating with the two-keeled posterior bracteole and the bract, *i. e.* being transversely placed. The two variations of the 2-merous flowers may be explained as follows: When the two perianth-leaves of the first whorl arise in the transverse position, they clearly constitute a 2-merous simultaneous whorl, alternating with bract and bracteole. In the 3-merous outer whorl, however, the leaves arise as usual successively, the two first ones, according to Payer and Schumann, behind, and in front of the two-keeled bracteole (which arises with two lateral rudiments), the third one much later and anterior. When this whorl becomes 2-merous, retaining, however, the successive mode of origin, so that the distichous arrangement is brought about, then the first perianth-leaf is posterior and the second opposite to it and anterior. Herewith we obtain transitions from the original 3-mery to 2-mery in such a way that the first leaf represents a double-leaf (leaves one and two of the 3-merous whorl united)."

The main reason why the posterior leaf is in front of the bracteole must be sought in the fact that in reality this latter represents two leaves which have recently fused.

The excessively reduced flowers (1-merous in one or two cases), observed by Magnus, Prillieux, and Stenzel (placed in the following section) are naturally followed by those in which all or most of the whorls are entirely suppressed, and if any one is left it is quite vestigial. Examples are afforded by the cauliflower and broccoli, in which, owing to excessive hypertrophy of the pedicels, the flowers are not developed, or only a vestigial calyx. In the feather-hyacinth (*Muscari comosum*), again, owing to the inordinate and copious branching of the pedicellar system, the flowers are almost entirely suppressed. The two cases mentioned are sports or abnormalities. But normally precisely

the same phenomenon occurs, as in the tendril of the vine, which is an inflorescence modified to serve as a climbing organ, and in which the tips of the pedicels have become hypertrophied in order to serve as adhesive disks.

1. SEPALS.—The phenomenon of *synsepal*y will first be referred to. This may be partial or complete.

In the pansy (*Viola tricolor*) incomplete fusion (the double sepal being forked) was observed between the two lateral anterior sepals; this had a curious effect on the petal opposite this double sepal: owing to lack of space its spur was turned inside out, thus appearing on the upper instead of on the lower side of the petal. It is not infrequent in orchids, as in the late spider-orchid (*Ophrys Arachnites*) observed by Penzig, in which the two lateral sepals were fused together, the single sepal so formed becoming opposite to the odd sepal. In *Cypripedium* this same fusion is the normal feature. Jaeger mentions a rare phenomenon in *Clematis Viticella*, all the petaloid sepals being united to form a campanulate structure, which was sometimes distinctly two-lipped.

Magnus observed in the orchid *Trichopilia* a 1-merous calyx consisting of a posterior sepal, enclosing, on the opposite side of the flower, a single petal which was not labelliform; hence this probably consisted of the fusion of the two lateral petals, and if so the single sepal probably arose from fusion of the lateral sepals, accompanied by suppression of the "posterior" one (Pl. LI, fig. 9).

Prillieux observed in *Epidendrum Stamfordianum* a 1-merous calyx of one posterior sepal, opposed to and enclosing a single anterior petal which was a labellum; this being so, the two lateral petals were clearly suppressed; hence it is probable that the single sepal represented the odd "posterior" sepal and that the two lateral ones were suppressed.

Stenzel describes a highly reduced flower of *Orchis globosa* in the axil of a bract a short way below the

inflorescence; it consisted solely of a single notched sepal formed by fusion of the two lateral ones; its dorsal side was directed towards the axis. In the early purple orchis (*O. mascula*) he saw a similar case.

Gamosepaly is, of course, a normal feature in the Gamopetalæ.

We may next consider instances of *suppression*. In *Cucurbita* in a 6-merous flower two sepals were seen fused together and one was vestigial, leaving four.

In *Cypripedium insigne* a 2-merous flower showed the complete absence of the "posterior" sepal owing to the abnormal presence in that position of a labellum. The flowers above-mentioned of *Epidendrum* and *Trichopilia* involved in their structure suppression of sepals.

In *Dendrobium Wardianum* the same phenomenon occurred; the two lateral petals had become united and occupied the position of the "posterior" sepal. All the flowers of the plant were affected in the same way (Pl. LIII).

The small secondary flowers, axillary to the sepals of the primary flower, in a cyclamen, had the calyx composed of two sepals only, and these were much reduced.

2. PETALS.—One of the best-known and most remarkable instances of sympetaly occurs in a variety of the Oriental poppy (*Papaver orientale*) in which the corolla forms a large cup, due to union of the four petals; there is a slight tendency towards fusion of the petals in the normal flower (Pl. LI, fig 10).

In the large group Gamopetalæ the phenomenon is, of course, the normal feature.

The gamophyllous condition of the perianth is of progressive nature. The Gamopetalæ represent the most advanced in evolution of all plant-groups.

Those phenomena are next to be mentioned in which some, but not all, of the petals become coherent.

The case of *Dendrobium Wardianum* has been cited above in which the two lateral petals became united

to form a "posterior" petal, its compound nature being shown by the conspicuous apical notch. An interesting example was seen in *Dendrobium* sp.; an incompletely 2-merous flower had two sepals, fore and aft; and two petals; of these there was one normal lateral one, and another in the position of the labellum, but its insertion extended round to that of the other lateral petal, so that it can be easily pulled round into that situation without any strain; it had also in part the colour of a labellum and in part that of a lateral petal; hence it clearly represents a fusion between the two.

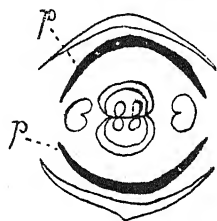


FIG. 151.—*Fraxinus dipetala*. Diagram of normal flower with two petals (p).

It is probable that in many other instances of a 2-merous corolla fusion between two petals has occurred. The same is true of many 4-merous corollas: in the pansy in which a 4-merous calyx had arisen owing to fusion of the two anterior sepals, the corolla was also 4-merous, and it is probable, although no direct evidence for it was seen, that in this whorl also fusion between two members had occurred.

Velenovsky describes flowers of *Forsythia viridissima* in which the four petals were fused in pairs to form a 2-merous corolla of two lateral petals; the calyx had the form of four green leaves (Pl. LI, fig. 11). It is interesting to note, as he points out, that the genus *Fraxinus* (ash) has a species (*dipetala*) in which, as the name denotes, the presence of two petals only is normal (fig. 151). Velenovsky observed in a flower of the rock-cress (*Arabis alpina*) that the petals had

fused in pairs to form a 2-merous corolla, the resulting two petals being in the antero-posterior position, and thus alternating with the two stamens of the outer whorl.

In *Veronica Buxbaumii* Camus found a flower with two petals* only, these being in the antero-posterior position; this represents a further advance in the evolution of the flower towards the 2-merous condition. Camus says that the Caucasian *V. Crista-Galli* has two sepals only as a normal feature. In the majority of species the corolla is normally 4-merous, due to fusion of the two posterior petals; and a point to be noted is that the resultant structure is by no means always larger than the lateral petals, but sometimes equal in size to, and even smaller than, these.†

Magnus describes the various forms assumed by the very small, more or less vestigial flowers which occur, as a rule, close below the large terminal peloric flower in the foxglove (*Digitalis purpurea*); their exceedingly reduced structure and size is due to the absorption into the terminal flower of the greater part of the food material. Of these the form which appropriately comes under this heading need only be cited.

In flowers consisting of a corolla only, which was monomerous (consisting of a single petal), was in the form of a closed tube, and either regular or irregular, one cannot say what the precise origin of this single petal was. Then there is the case observed by Magnus

* It is quite correct, in spite of what some systematists inform the writer, to speak of petals in these cases of gamopetalous corollas; for whatever happens, either in the way of fusion or division, to the corolla-lobes must be regarded as happening to the corresponding extension of them below in the tube.

† A well-known systematist informs the writer that a petaloid structure which is known to result from the fusion of two or more petals must always be regarded as a compound structure, as in the "lips" of Labiatae, and if the posterior petal of *Veronica* originates from a fusion of two petals, it must be regarded as two petals, not one. To this the writer must entirely demur; where the union is so intimate that all trace of the originally separate petals has been lost, the organ may be regarded as a single petal; still more is this the case where, as in some species of *Veronica*, the supposed compound petal is the same size as, or even smaller than, the others composing the whorl.

of a 1-merous corolla in an orchid mentioned under the previous heading, due to fusion of two lateral petals. A sketch was received from Mr. G. S. Saunders of a flower of *Cypripedium Selligerum* whose perianth consisted of a single anterior sepal and a single posterior petal, this having the form and consistence of a normal lateral petal (fig. 152).

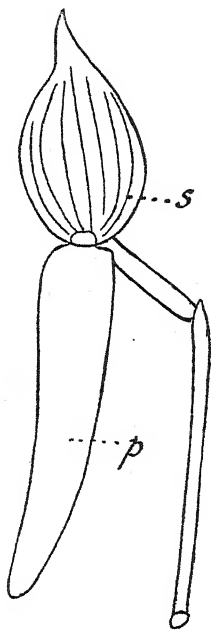


FIG. 152.—*Cypripedium Selligerum*. Flower with monomerous corolla. (G. S. Saunders.) s, sepal; p, petal.

Cases of *suppression* of the petals will next be noticed. A flower of the orchid *Calanthe vestita* was seen in which all three petals were absent. In a flower of *Selenipedium* the labellum was the sole representative of the corolla. In a *Kalmia* all flowers were entirely devoid of corolla, while the remaining whorls were present in their normal condition. On the other hand, the complete absence of the corolla in

Mimulus luteus var. was correlated with the petaloid development of the calyx. In the goldilocks-buttercup (*Ranunculus auricomus*) the corolla, either wholly or in part, disappears. Velenovsky found individual plants of *R. acer* in which the stamens were absent or abortive, this feature being accompanied by a tendency to abortion in the corolla. In the chickweed (*Stellaria media*) and the mouse-ear (*Cerastium vulgatum*) apetalous flowers sometimes occur, while this is the normal condition in a species of pearlwort (*Sagina apetala*) of the same order.

In the flowers observed by Prillieux and Stenzel in orchids the 1-mery involved suppression of certain petals; this was also the case with the labellum in the flower of *Cypripedium Selligerum* figured. In the flower of *Cypripedium superbiens* before-mentioned the fusion of the lateral petals with the posterior sepal to form a single large threefold leaf involved complete suppression of the labellum, an interesting example of how the law of alternation works.

Wakker found and figured a flower of the toadflax (*Linaria vulgaris*) whose corolla was quite normal except for the complete absence of a spur; this fact was due to the middle petal (not middle lobe only, as some systematists would assert), *i. e.* the median anterior one, being absent; for in these plants the spur is an outgrowth of this petal. In conformity herewith there were only four sepals; and it would probably be found (the author does not inform us further) that the reduction in this whorl, in accordance with the usual working of the law of alternation, was due to fusion of the two lateral anterior sepals to form a single one inserted opposite the gap left by the median anterior petal.

3. STAMENS.—*Synandry*.—Andersson observed fusion of the two stamens in *Salix calyculata*; and this is a normal feature in *S. monandra*, and precisely simulates the normal union of the two carpels to form the syncarpous ovary. A similar kind of union occurs normally

in Cucurbitaceæ. As a normal feature union of the stamens is not at all infrequent: *e.g.* monadelphly in Malvaceæ and Leguminosæ, diadelphly in Leguminosæ, polyadelphly in Hypericaceæ, etc.

In an otherwise normal andrœcium it sometimes happens that two or more stamens become fused, as in the 5-merous ones seen in the daffodil (*Narcissus Pseudonarcissus*), *Lilium*, etc., this condition being due to fusion between two of the members, probably one from each whorl. Celakovsky describes a very interesting case of this phenomenon in the flowering-rush (*Butomus umbellatus*); in the normal flower there are nine stamens, six in the outer whorl, grouped in pairs opposite the sepals, and three in the inner whorl opposite the petals. This arrangement is obvious during the first stage of development; at a later stage, however, the inner whorl becomes intercalated in the outer. In the abnormal flower it has happened, during the later developmental stage, that two stamens of the inner whorl have each become fused (for the whole or greater part of the length of the filament, but not in the anther-region) with a stamen of the outer whorl. There would thus appear in this instance to be two distinct steps in the blending of the two whorls into one. Normal cases of the same kind occur in the Fumariaceæ and in *Monsonia*.

The abnormally 4-merous flowers of *Pentas*, *Primula*, *Passiflora*, etc., as also many normal cases of 4-mery in Dicotyledons, may be attributed to fusion between two members of the whorl of five, this fusion being so profound as to leave no visible trace.

Kirschleger observed in some virescent flowers of the bleeding-heart (*Dielytra spectabilis*) two lateral stamens of the outer whorl, and in the second whorl two deeply-split filaments; the two branches of each filament bore monothecal anthers. So that in this case the monothecal stamens, instead of fusing, as in the normal flower, with the stamens of the outer whorl, had become united in pairs in the median plane. Hence a

distinct tendency is here manifested towards the formation of a 2 + 2-merous andrœcium. This, as Celakovsky indicates, is the normal condition in the genus *Hypecoum*, where however the fusion is complete, so that in the second whorl are two complete stamens. But Eichler has shown that in this plant the andrœcium begins its development as two lateral long-extended primordia, from which at both ends the rudiments of the four monothechal stamens separate off; after that they approach and fuse to form the median dithecal anthers. In both the normal developmental process of *Hypecoum* and the abnormal mature structure of *Dielytra* the tendency towards the formation of two whorls must be regarded as a reversion, but that towards fusion of the pairs of stamens in the median plane as a progressive, reductive phenomenon.

Velenovsky observed in the flower of *Arabis alpina* above-mentioned that the leafy stamens constituting the anterior pair of the inner whorl had fused into one. We thus see throughout this flower a very strong tendency towards the 2-merous condition, as in the *Fumariaceæ* just mentioned.

Suppression is a very common normal method by which numerical reduction in the andrœcium has been brought about. The whole subject has been elaborated by Celakovsky, to whose works the reader is referred. A few abnormal instances may be cited.

Streptocarpus (Gesneraceæ) normally possesses four stamens, two anterior and two posterior; a flower was seen which had only the two posterior ones.

Hildebrand describes a flower of *Mimulus luteus* in which the two anterior stamens only were present. It is the normal condition of *Veronica*, belonging to the same order, to possess two only, but these are in the posterior position.

Penzig cites Camus as describing a plant of the moth-mullein (*Verbascum Blattaria*) on which all flowers of the inflorescence had the fifth posterior stamen completely suppressed. This is a most interesting case as

affording a transition to the genus *Celsia* which only differs from *Verbascum* in having four didynamous stamens, instead of five more or less equal ones. Camus found suppression of one of the two stamens in various species of *Veronica*.

Warming and Battandier both found in the corn-poppy (*Papaver Rhœas*) and *P. malvæflorum* respectively, which were growing under very adverse conditions, that the polymerous androecium of the normal flower was reduced to four stamens, thus reproducing in a very interesting way the 4-mery of the corolla.

Flowers of herb-Paris (*P. quadrifolia*) have occasionally been observed in which all whorls were 3-merous.

Masters mentions a flower of *Cypripedium* in which, while stamens a^1 and a^2 of the inner whorl were normal, the staminode of the outer whorl was absent. This may be aptly compared with the condition in *Adactylus* whose normal androecium is exactly the same as the abnormal one in the *Cypripedium* just mentioned. *Adactylus* belongs to the allied tribe Apostasiæ. In *Apostasia* the staminode has almost disappeared, having the form of a filamentous structure adnate to the style.

Finally, there are those cases in which all the stamens are suppressed, inducing of course thereby unisexuality of the flower. This is a progressive change and not reversionary, for originally all flowers were hermaphrodite or bisexual.

Velenovsky observed otherwise quite healthy plants of *Ranunculus acer* in which all the flowers were two or three times smaller than usual, and the petals of each also smaller; the stamens were represented only by insignificant papillæ below the pistil.

In some apetalous flowers of *Mimulus luteus* in which the calyx had become petaloid, both corolla and stamens were quite absent. There are many cases known where suppression of the androecium has occurred without the advent, so far as could be ascertained, of any special stimulus which might have induced it, as in the *Ranunculus* above cited.

In other instances the reason of the suppression is quite obvious, and lies in the diversion of the necessary nutriment in order to form new and extra structures which do not occur in the normal flower, as in the *Mimulus* just mentioned. A similar example was seen in a double flower of the common stock (*Matthiola*) which had proliferated above the insertion of the corolla into an inflorescence, both stamens and pistil being on that account entirely suppressed.

Normal examples of unisexuality are very numerous, and have been derived from the bisexual condition.

4. CARPELS. — *Syncarpy*. — As the syncarpous character of the pistil is by far the most frequent under normal circumstances, great frequency of this feature as an abnormal occurrence is precluded.

The few cases known are special ones. In *Amygdalus* and *Prunus* there is occasionally to be found an increase in the number from the normal single one to from two to five carpels; this is accompanied by fusion of the carpels to form a syncarpous ovary like that of the Pomeæ.

When, in the scarlet runner (*Phaseolus multiflorus*) or kidney bean (*P. vulgaris*), two to three carpels in place of the normal single one appear, these are often either partially or completely united to form a syncarpous pistil. The same thing has been observed in the garden pea (*Pisum sativum*) and *Gleditschia*.

In the St. Valéry apple the ten stamens, during their transformation into carpels, become united to form a syncarpous ovary perfectly resembling the normal one in the tier below.

Fermond mentions that in *Delphinium elatum* several carpels were coherent, whereas normally the pistil consists of discrete follicles. The same thing has been noticed in *Helleborus*. Now this union of the carpels, be it observed, is the normal feature in love-in-a-mist (*Nigella*).

Some instances of reduction in the pistil are due to intimate fusion of two or more carpels. A very

interesting transitional example was seen in *Lilium candidum* which proved this. The different whorls, as described in a previous section, were rearranging themselves during the tendency towards spiral phyllotaxis; two members of the perianth, a sepal and a petal, had become united, as also two stamens, one from each whorl; of the three carpels two were partially coherent, representing a transition to two carpels.

Suppression.—In the normal course of floral evolution, as Celakovsky has so well pointed out, great numerical reduction in the gynœceum has taken place, in fact much more so than in any of the other whorls. This is well seen in the Prunæ section of the Rosaceæ and in the Leguminosæ.

The pleiomerous gynœceum may become abnormally reduced. Masters mentions a flower of *Papaver Rhœas* which was evidently provided with four carpels only.

Moquin Tandon states that a bramble (*Rubus*) produced an etærio with but a single drupelet, resembling a small cherry.

The pistil of *Aconitum*, *Delphinium*, *Nigella*, and *Pæonia* has doubtless been evolved from one with many carpels, as in the majority of the Ranunculaceæ; in these meiomerous pistils reduction still frequently occurs abnormally.

In the flower of *Tulipa persica* previously described, which had a 5-merous perianth and androecium, the pistil was bicarpellary.

A long list of such instances of reduction need not be cited; they are sufficiently numerous.

A rather striking one may be mentioned in the 2-merous orchid- and *Iris*-flowers, where the normal 3-merous ovary loses a member of its whorl. Also in the flower of *Odontoglossum crispum* in which disruption of the column and petalody of some of the stamens occurred, the ovary and stigmas appeared to have completely vanished.

There is the interesting example of a garden tulip (*Tulipa Gesneriana*) observed by Roeper, in which, obviously owing to the carpelloid transformation of the inner whorl of stamens, the normal carpels had become suppressed. This explanation is more probable than that the inner whorl of stamens was suppressed and the carpels had become rearranged in order to alternate with the stamens of the outer whorl.

GENERAL CONCLUSIONS.

The majority of botanists in the past have subscribed to the view that the pleiomerous condition of the flower is the more recent, the oligomerous the most primitive phenomenon in any given order or group of plants. For example it was held that in the Cruciferae the dimerous condition was the original one from which the pleiomerous condition (as in the andrœcium) of other genera and of Capparidaceae was derived by fission of the stamens. This view appears to have been based largely on the facts of ontogeny observed in such orders as the Cistineae and Hypericaceae, in which the groups of numerous stamens were each seen to branch from a single rudiment. Protagonists of this view are De Candolle, Eichler, Delpino, Engler, and Velenovsky. In recent years, however, what is probably the more rational view has been set forth, mainly by Celakovsky, that the opposite is true, namely that the pleiomerous condition is the more primitive of the two. So that a flower like that of *Calycanthus* or *Nymphaea*, with numerous members in all the whorls, would stand for the most primitive type. Two main facts are strongly in favour of Celakovsky's view: firstly, that many orders, for other reasons regarded as primitive, often have pleiomerous sexual whorls, the members being arranged in spiral series, *e.g.* Ranunculaceae, Nymphaeaceae, Magnoliaceae, and Palmaceae; secondly, that the process of reduction is so widely observable as having occurred in the past that

one is driven to the conclusion that it has been one of the main factors in the evolution of the flower.*

The crux always arises over the transitional cases, *e. g.* in the Cruciferae that of the four stamens of the inner whorl which are grouped in pairs; the ontogeny shows that at the earliest stage the pair of stamens is represented by a single one, which only at a later stage branches into two. Eichler, guided by these facts of ontogeny, and by the fact that occasionally a single stamen replaces each pair, holds that the 2-merous condition of both whorls was the original one, and that the pairs of the inner whorl have arisen later by positive *dédoublement*.

Celakovsky's view is, on the contrary, that the approximation of the stamens in pairs is due to negative *dédoublement*, that what has occurred already in the outer whorl is at present occurring in the inner whorl, viz. a progression towards dimery of the andrœcium.

Velenovsky holds that the Rhœadales are founded on a dimerous type derived from the immediate ancestry. This is proved, he thinks, by such a fact as the 4-merous andrœcium observed in *Papaver* by Warming and Battandier, that of the normal flower, as in the Capparidaceæ, being a more recent reversion to the pleiomerous condition of the still remoter ancestry. But these poppies were growing under specially impoverished conditions which would act as a further stimulus to the already present tendency in the order Papaveraceæ for reduction in the various whorls. Velenovsky admits the remote ancestral nature of the normal pleiomerous andrœcium, but it

* Wernham ("Floral Evolution; with particular reference to the Sympetalous Dicotyledons," 'New Phytologist,' vol. x, April, 1911) brings out the interesting fact that "whereas the flowers of barely 20 per cent. of the total number of species of Archichlamydeæ have stamens equal in number to, or less than, the corolla segments, an isomerous or oligomerous andrœcium characterizes nearly 95 per cent. of the species of Sympetalæ. Only about 18 per cent., again, of the Archichlamydeæ have a pistil composed of two syncarpous carpels or, in some rare cases, of one only; in the Sympetalæ, on the other hand, fully 75 per cent. of the species have flowers with a bicarpellary gynœceum." The Sympetalæ are universally regarded as a more advanced group than the Polypetalæ.

seems quite as reasonable to suppose that the ancestral condition has been preserved all along as that it has once been submerged and again resurrected. Further, the obvious relationship of the Papaveraceæ to the Polycarpicæ subverts this idea.

Abnormal changes in the direction of simplification and reduction, *i. e.* in the direction of evolution, are quite frequent. The very common 2-merous flowers of orchids afford a good instance of a progressive abnormality.

Velenovsky regards the abnormal 2-merous corolla of *Forsythia*, mentioned on a former page, as a reversion to the immediate ancestry which exhibited 2-mery in all floral whorls. But in the closely allied genus *Fraaxinus* there is a manifest process of reduction obtaining in the corolla, for this is completely absent in the common ash (*F. excelsior*). The 2-merous corolla of *F. dipetala* Velenovsky marshals, on the flimsiest of grounds (that of the common occurrence of 2-mery in the order), in favour of 2-mery being the primitive condition; it is, on the contrary, best regarded as a half-way stage between the 4-merous corolla of the manna ash (*F. Ornus*) and the completely suppressed one of *F. excelsior*. This is strongly supported by the fact that in the majority of Oleaceæ the 4-merous corolla of *F. Ornus* obtains. In any case the completely suppressed corolla of *F. excelsior* can be regarded in no other light than as a very recently-acquired feature. If, then, reduction has occurred in this species, it is most probable that this is the cause of the condition in *F. dipetala*. There are thus two valid reasons for regarding the 2-merous condition of the corolla in this order, whether normal or abnormal, as a progressive and not a reversionary phenomenon. If this be true of the corolla, it is also almost certainly true of the andrœcium, and the 4-merous andrœcium of *Tessarandra* (belonging to the same order) must be regarded as more primitive than the much commoner 2-merous one. If the 2-merous condition is a pro-

gressive feature in the Orchidaceæ and Oleaceæ, the probabilities are in favour of this condition being also progressive, and not reversionary, in all other orders where it obtains, *e. g.* Cruciferae and Papaveraceæ, for the law of reduction reigns universally throughout the Angiosperms.

Hence, Celakovsky would appear to be right in holding that the most primitive type of flower is that in which the pleiomerous condition prevails in all parts of the flower, and in which the floral leaves, from calyx to pistil, are arranged spirally and not in verticils. The abnormal increase in the number of whorls and of members composing them must therefore be regarded as, in the great majority of cases, due to reversion to an ancestral condition. In the case of the tulip and lily the dual tendency was manifest to revert to a larger number of members and to the spiral arrangement thereof; the $4 + 4$ condition of the tulip corresponds to the spiral series $\frac{2}{8}$, the $5 + 4$ to the series $\frac{2}{6}$, the $4 + 3$ (so common in the androecium) to the series $\frac{2}{7}$. The Monocotyledonous flower of the ordinary type, *e. g.* the tulip, has almost certainly been reduced from a more complex type, probably from that found in such plants as the Berberidaceæ and Magnoliaceæ in which both calyx and corolla have more than one whorl of three. For instance, the $K5 C5$ of some tulip- and lily-flowers (really representing in each whorl a congestion of two: $K2 + 3 C2 + 3$) has nearly reached the presumed ancestral condition which is to-day exemplified in Berberidaceæ, etc.: $K3 + 3 C3 + 3$. From this the typical Dicotyledonous flower is but one step removed by reduction, the floral formula being: $K5 C5 A5 G5$, which is that of our pentamerous tulip. In the typical Dicotyledonous flower the whorl of five probably represents a congestion of two whorls of two and three each, a fact which is generally recognized, at any rate for the calyx.

We may conclude, therefore, that both in the normal and the abnormal phenomena in which reduction,

whether by fusion of two or more organs together, or by suppression of one or more organs,* has occurred, this is in all cases a progressive or evolutionary event. In the first case it results in the production of one organ where before there were two or three, and where such a fusion is complete, as in many instances of the median posterior petal of *Veronica*, the resultant must no longer be regarded as double, *i. e.* as embodying within itself the two or three original organs, but as a unity, for the union which brought it into existence is not a fusion to form a compound organ but a complete unification, which implies as perfect an extinction of the individuality of the original organs which took part in the fusion, as does the suppression *in situ* of any single organ of the flower.

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* It may be doubted if the regular alternation of whorls, implied in these two processes, has a wholly adaptational significance; it may in part be regarded as the expression in the flower-structure of a basic law of nature, viz. that of rhythm, activity constantly succeeded by quiescence, the wave-motion to which no biological cause may be attached.

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III. ADVENTITIOUS FLOWERS.

These are rare. They have occurred in the ovary of the lady's-smock (*Cardamine pratensis*) near the place of origin of the ovules. Masters figures a remarkable instance of a flower arising in the position of an ovule in the pod of a wallflower; it consisted of an ovary only, there being no sign of stamens or floral envelopes.

He also figures a grape containing small, entire, stalked grapes within it in the position of seeds (fig. 153).

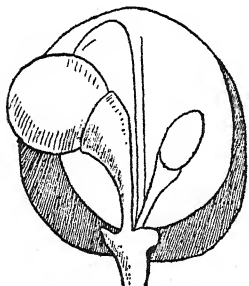


FIG. 153.—*Vitis vinifera* (Grape). Longitudinal section of fruit, showing two adventitious grapes in the position of seeds. (After Masters.)

Perhaps the most remarkable case of all, *i. e.* if it really comes under this heading (where it may be provisionally placed until the phenomenon is satisfactorily explained), is afforded by the Nepaul barley (*Hordeum caeleste trifurcatum* or *H. trifurcatum*). This peculiar structure was thoroughly examined by the present writer, and it has been described by many authors in the past. It is enough to transcribe here the account of it given by Penzig.

"In all spikelets the inferior pale [bract] (much more rarely the superior pale as well) shows a very peculiar form: instead of, as is usually the case, tapering and terminating in a long awn, it has at the

tip a kind of hood-shaped appendage which is directed outwards almost at right angles to the pale. Right and left of this spur-like appendage the margin of the pale is produced into two more or less long, triangular or awn-like teeth. The inwardly-recurved apex of

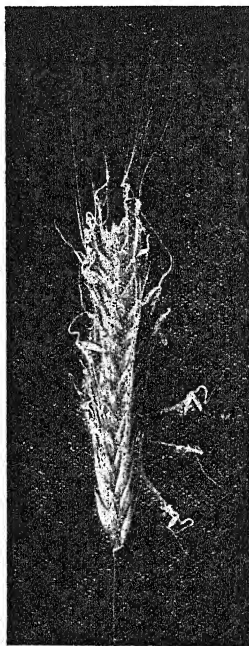


FIG. 154.—*Hordeum trifurcatum* (Nepaul Barley). Ear bearing spikelets with adventitious flowers. (S. Garside photo.)

the hood-shaped appendage may (in some varieties) be produced into a more or less stout awn." "On the inner side of the hood-shaped extension there may often appear small scales, arranged distichously on a short axis, and between which, in many cases, flower-rudiments arise. Wittmack saw in the variety *Horsfordianum* complete fertile flowers and ripe grains arising in the extension of the pale" (figs. 154 and 155).

It would thus appear, from the purely outward

appearance of the structure, that we have to do in this case with a spikelet arising adventitiously on the upper surface of the tip of the inferior pale (bract of the flower, according to the view here held). At any rate this is the view which has been generally adopted. As Penzig points out, however, Raspail observed the separation of the awn-bearing midrib from the inferior pale (in several grasses) as a short floriferous axis. Hence the anomaly may merely consist in fusion of an axillary product with its subtending bract.

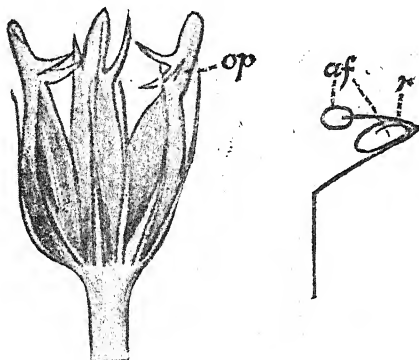


FIG. 155.—*Hordeum trifurcatum* (Nepaul Barley). Three spikelets showing the trilobed apex of outer palea of each (*op*). Diagram showing reflexed rachilla (*r*) within the hood bearing two adventitious florets (*af*). (After Masters.)

Above are cited three cases of adventitious flowers occurring on foliar organs, viz., on carpels and a bract.

There must now be mentioned two instances of their occurrence on the floral axis. The first was in a carnation-flower, sent by the editor of the 'Gardeners' Chronicle,' which had proliferated into a second flower whose calyx consisted of the carpels of the first; the petals of the primary flower, which was double, were replaced by numbers of very small flowers consisting entirely of petaloid organs; these flowers, not being axillary, must be regarded as adventitious.

Some hypertrophied female catkins of the crack-

willow (*Salix fragilis*)* were examined, in which the bracts and pistil were enlarged and virescent, and slight proliferation of each flower had occurred. But the striking feature about all, or the majority of the flowers, was the fact that, all round the base of the ovary, on the floral axis above the level of the bract, were great numbers of separate carpels, occurring either singly, or aggregated in places into distinct outgrowths, their distribution being altogether irregular, and the individual carpels varying in age and size. They must be regarded as representing masses of rudimentary flowers which have not been able to develop in the normal rigid way owing to the excessive vigour of the tissue-growth of the axis; hence they are also adventitious and not axillary.

On some woody twigs of the same species the entire catkins appeared to be represented solely by dense agglomerations of these rudimentary flowers which were arising endogenously from the inner tissues of the cortex, and breaking through the bark at four different places, causing as many longitudinal slits in the twigs. The endogenous formation of flowers is a hitherto unheard-of phenomenon and is one of the very rarest abnormalities to be met with.

These hypertrophied catkins are probably due to the irritation set up by aphides or mites.

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* Sent by Mr. Hugh Watt, of Hampstead. The present writer collected specimens of the same abnormality on some trees of this species at Chingford, also of this species and of *S. alba* and *S. viminalis* on Hampstead Heath.

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FINAL CONCLUSIONS.

So many general conclusions have been drawn in connection with most of the various sections of this work, and so many general statements have been made bearing on the meaning and origin of the different abnormal structures concerned, that hardly any further statement is required at the conclusion of the whole.

The conviction may once more be reiterated that the vast majority of these abnormal structures are not accidental or freakish in nature, but are produced by the working of the same laws which govern the up-building of normal structures; and that most of the abnormalities are but reproductions, modified according to the idiosyncrasy of the present types which exhibit them, of normal structures which either exist to-day in other sections of the same group, or have existed in the ancestry and have since become extinct.

The modern tendency to neglect the study of abnormal forms as a guide to the solution of morphological problems, as also the wavering interest of botanists of the present day in the subject of comparative morphology itself (there being a greater concentration

on mendelism, physiology, and ecology), is probably due to the fact that a growing interest and craving is to be found for the study of the living organism as such; the various forms which it may assume during life, or which it has assumed in the past, seeming to be of less striking interest than the functions which those forms exist to subserve. Hence the abnormal structures, whose function is either unknown, non-utilitarian, or even destructive for the plant concerned, are ignored by the typical botanist of the day, interested mainly, as he is, in the departments above mentioned. Nevertheless, there cannot be a shadow of doubt that, regarding the science of botany as a whole, and from the broadest standpoint, the subject of Comparative Morphology, including that of its sub-section Teratology, is every whit as important as any other department of the science, and it was to afford some indication of this that these volumes have been written.

SUMMARY.

The volume is divided into three main sections: Differentiation, Simplification, and Adventitious Flowers.

Under the heading of Differentiation are grouped the following phenomena.

Proliferation: this is of two kinds, viz. median and axillary. The former concerns the main axis of the inflorescence or flower, the latter the lateral outgrowths. Both kinds may be either reproductive or vegetative. It is a reversionary phenomenon.

Forking and Fasciation: these are essentially the same phenomena as have been described for the Stem. There is no real difference between normal and fasciated inflorescences and flowers. As in the stem, there are two types of fasciation, ordinary and ring-fasciation. The latter is due, morphologically, to lateral invagination of the external parts. Both kinds represent stereotyped stages in the division of the inflorescence or flower.

Disruption: this consists in the splitting of the maize-cob, or female inflorescence, into its primitive constituents or branches which had become fused together to form the "cob." The result is a paniculate inflorescence resembling the male one.

Positive Dédoublement: this is "polyphyly," the increase in number of the members of a whorl, or "pleiotaxy," the increase in number of the whorls. The tendency of an organ to divide overrides the tendency towards unity. It is described with reference to all the floral whorls and to the sporophylls of Cryptogams. The phenomenon is generally a reversionary one.

Dialysis: the dissociation of members belonging both to the same and to different whorls. A reversionary phenomenon.

Metamorphosis: the "Flower" has been evolved from an elongated leafy shoot, with the "cone" as an intermediate stage; an analogous example of the process is seen in the Pteridosperm—*Bennettites*—Cycad phylum. The changes concerned, as they affect the four floral whorls and the sporophylls of Cryptogams, are Phyllody, Squamody, Bracteody, Sepalody, Petalody, Zygomorphy, Pelory, Staminody, Carpellody, and Sporangiody. Among the subjects discussed are the morphology of the "corona" in Amaryllidaceæ, and that of anther-structure. Many phenomena under this heading are reversionary, while others are progressive.

Under the heading of Simplification are included: (1) Abbreviation of the inflorescence and flower; this is the opposite condition to proliferation; (2) adnation of floral axes, either with each other, or with floral leaves; or the adnation of floral leaves; (3) cohesion, including synanthly or the union of entire flowers; and negative dédoublement, in which the tendency towards fusion overrides that towards division; (4) suppression, representing the final stage in the reduction-process, in which floral members or whorls become completely eliminated. Negative dédoublement and suppression are considered with reference to the various floral whorls.

Simplification of the flower by means of cohesion and suppression of its members represents one of the main processes of floral evolution. The tendency towards division and multiplication, as shown here and there in the ontogeny of floral members, is a reversionary phenomenon.

Adventitious flowers and fruits are finally described, and special attention is drawn to the occurrence of endogenous flowers in *Salix*.

ADDENDA TO VOL. I.

THE LEAF.

FORKING.

The writer has received from Dr. E. J. Salisbury, and has also himself obtained from seed, seedlings of the maize (*Zea Mäis*) having the coleoptile bifurcated for some distance from the apex. The fact that the normal coleoptile possesses two widely-separated veins of equal strength is itself almost sufficient to indicate its compound nature. The abnormality tends still further to show that this organ consists of two fused foliar organs, and yields evidence in support of the view, already strongly suggested by the position of the coleoptile immediately in front of the scutellum, that this organ represents the "ligule" of the scutellum (cotyledon), *i. e.* its fused stipules. Bifurcated ligules have occurred on the foliage-leaves of grasses.

ENATIONS.

A cabbage-leaf, sent from a Surrey garden, had its upper surface covered with multiform enations. Great numbers of the ultimate ramifications of the cresting were almost the exact counterparts, as regards their conformation, of virescent ovules such as have been described by Celakovsky.

ADDENDA TO VOL. II.

THE FLOWER.

PROLIFERATION.

A narcissus was seen in which proliferation of the flower-stalk *above the spathe* had occurred to form a stem equal in length, and otherwise similar, to that of the plant between the bulb and the spathe; it bore at the top a normal spathe and flower. In another specimen the spathe subtending the proliferated flower-stalk was excessively elongated, enveloping the stalk almost to the apex.

DIALYSIS.

Partial dialysis of the corolla was observed recently in a white foxglove (*Digitalis purpurea*). The two posterior petals were still normally united, a lateral one was united at the base with the large posterior petal, while the two remaining petals were free. One or two stamens were free from the corolla.

METAMORPHOSIS: HETEROSEPALODY.

As showing that the spur in the Indian cress (*Tropæolum majus*) is part of a sepal, and not of the receptacle, a flower belonging to Col. Rawson was seen in which a foliaceous sepal bore a spur situated well above its base.

METAMORPHOSIS: SEPALODY.

Some apples were received from Miss E. A. Portal, of Over Wallop, Hants, in which the corolla and some of the stamens had become transformed into sepals, each with a swollen fleshy base like the normal ones constituting the pome below. Withered remains of some stamens and styles occurred in the "eye" at the top. The axis in the base of the pome had slightly elongated, carrying the core, which was poorly developed and contained a few withered undeveloped pips, to the top of the fruit. The fruit is stated to be in some cases more elongated and conical.

It is not unlikely that the phenomenon here described is the same as that shown by the abnormal pears detailed in a previous section under "Proliferation." If so, the theory of Wittmack with regard to the "storeyed" pears must be held to be the correct one, viz., that the "storeys" represent corolla, andrœcium, and styles respectively, changed into sepals. And the theory propounded in this work, that they represent secondary and tertiary pears due to proliferation, must be given up.

The appearance presented by such an apple as this is a most unusual and peculiar one. It shows the same phenomenon as that exhibited by the seedless Colorado apple described on pp. 13-14, but in that case the corolla only had undergone the change.

METAMORPHOSIS: PETALODY OF STAMENS.

A flower of a rhododendron (*Ascot Brilliant* × *Thomsoni*), sent to Kew by Sir E. G. Loder, showed a deviation rare in this plant. The withered corolla bore curious fleshy, crimson, waved outgrowths at its base; the axis of the flower was somewhat elongated, and all the stamens, save one or two, changed, wholly or partially, into large petals, of which the lower were free, the others united to form gamopetalous hose-in-hose corollas; they had also increased in number. The flower was more than two months out of season (late), and had developed from an axillary, not a terminal, bud.

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- Zygopetalum*, staminody of petals, 160.

ERRATUM.

P. 124, line 4, for *Dionæa* read *Dionæa*.

ADDENDA TO ERRATUM IN VOL. I.

P. 37, line 4, for 4 read 1.

Plate IV, fig. 3, *b* and *c* are of *Marchantia*, not *Lunularia*.

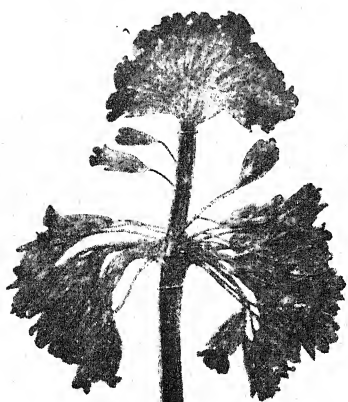
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PLATE XXVI.

FIGS.

- 1, 2. *Primula veris* (Cowslip). Proliferation of the inflorescence. (J. Hutchinson photo.) p. 3.
3. *Lupinus polyphyllus* (Lupin). Proliferation of the inflorescence into a leafy shoot. (J. Hutchinson photo.) p. 6.

PLATE XXVI



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PLATE XXVII.

Figs.

1. *Larix leptolepis* (Larch). Proliferation of female cones into leafy shoots. (G. E. Massee photo.) p. 5.
2. *Plantago major* (Great Plantain). Proliferation of flowers of spike into paniculate inflorescences. (G. E. Massee photo.) p. 6.
3. *P. lanceolata* (Ribwort). Proliferation of lower flowers of spike into secondary spikes. (Original.) p. 6.

PLATE XXVII





Plate 28

PLATE XXVIII.

FIGS.

- 1-3. *Pyrus communis* (Pear). Figs. 1, 2.—Proliferation to form a second pear whose fleshy sepal-bases (*s*) have become dissociated. (Original.) Fig. 3.—A pear consisting of two sepals only, each with a slightly swollen base. (Original.) p. 10.
4. *Rosa damascena* (Garden Rose). Proliferation of flower into a second flower. (After Turpin.) p. 7.

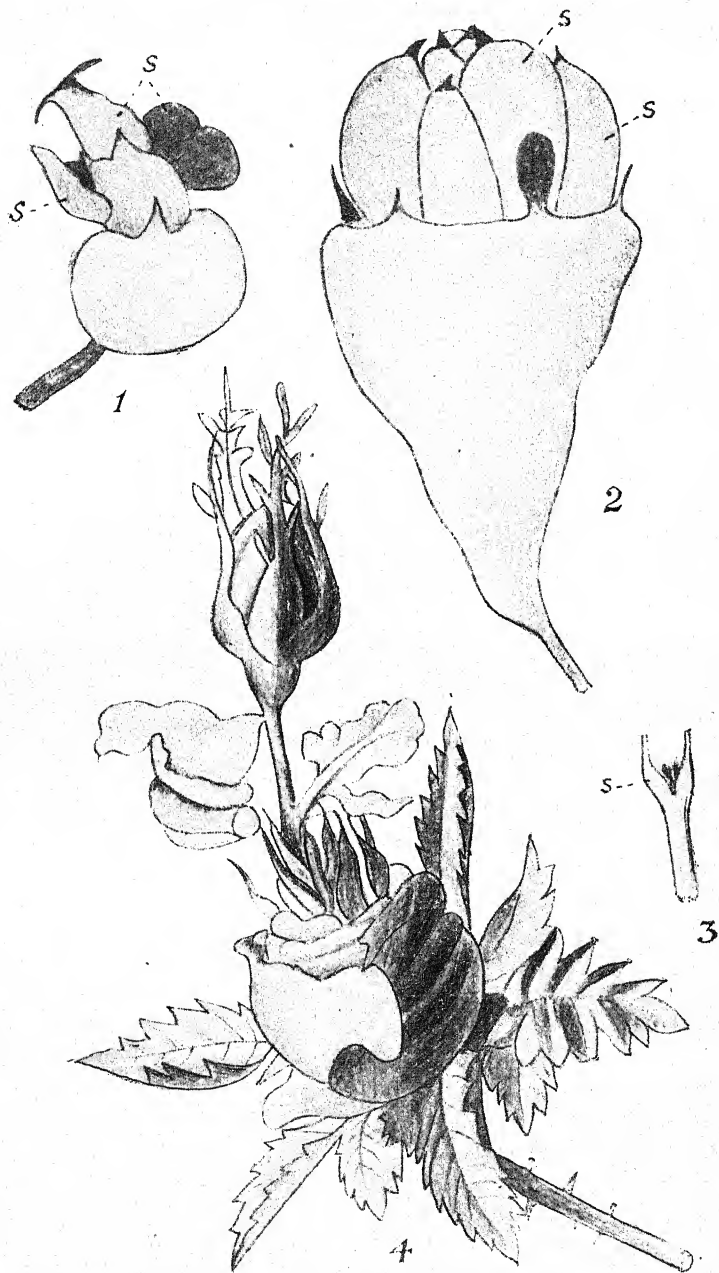


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PLATE XXIX.

FIGS.

1. *Euphorbia Cyparissias* (Cypress Spurge). Glandular bracts scattered on elongated axis of inflorescence. (After Schmitz.) p. 4.
- 2, 3. *Dianthus barbatus* (Sweet William). Flowers all proliferated into bract-bearing axes. (G. S. Saunders.) p. 17.
4. *Pyrus communis* (Pear). Fruit proliferated into a vegetative shoot. (After Sorauer.) p. 17.
5. *Celastrus scandens*. Each petal with a flower in its axil. (After Turpin.) p. 21.

PLATE XXIX



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PLATE XXX.

FIGS.

1. *Rosa damascena* (Garden Rose). Flower proliferated into a vegetative shoot. (Original.) p. 17.
- 2, 3. *Scabiosa atro-purpurea*. Fig. 2.—Proliferation of terminal floret of capitulum into a virescent floret (s, sepals). (Original.) Fig. 3.—Section of the whole. p. 17.

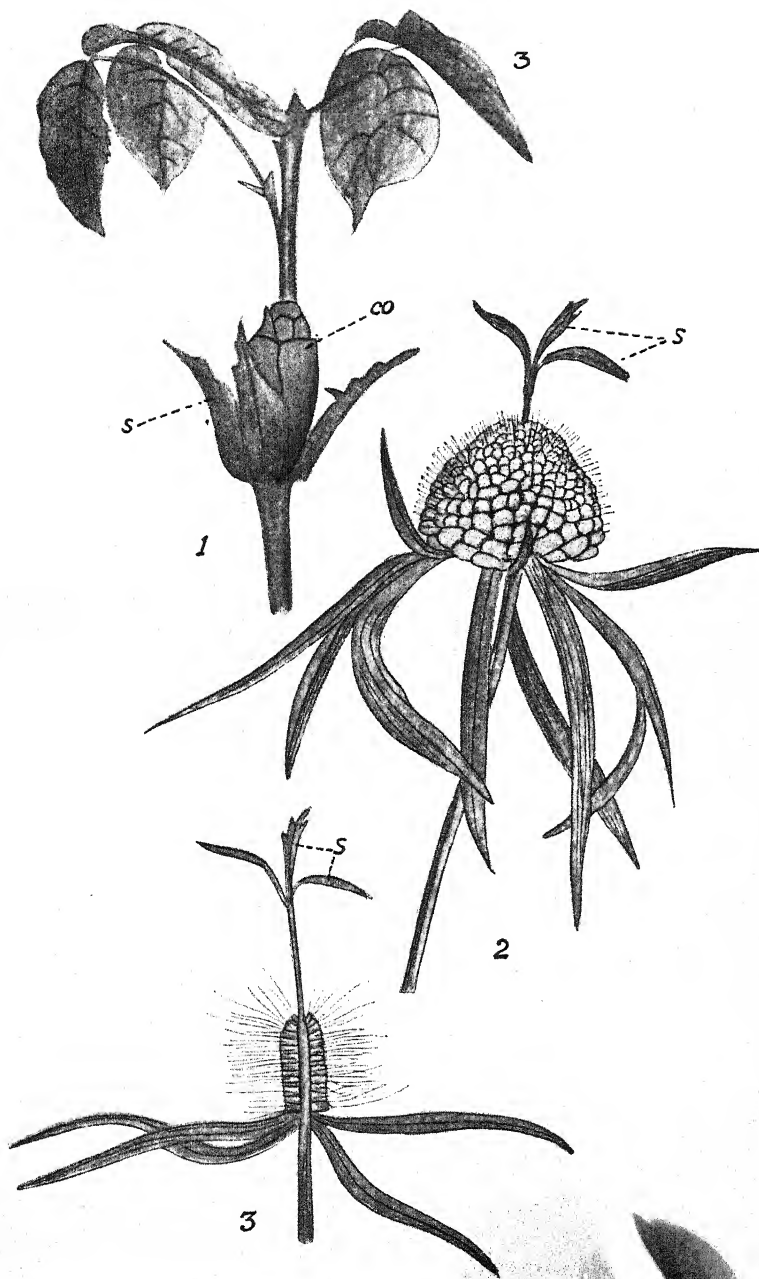


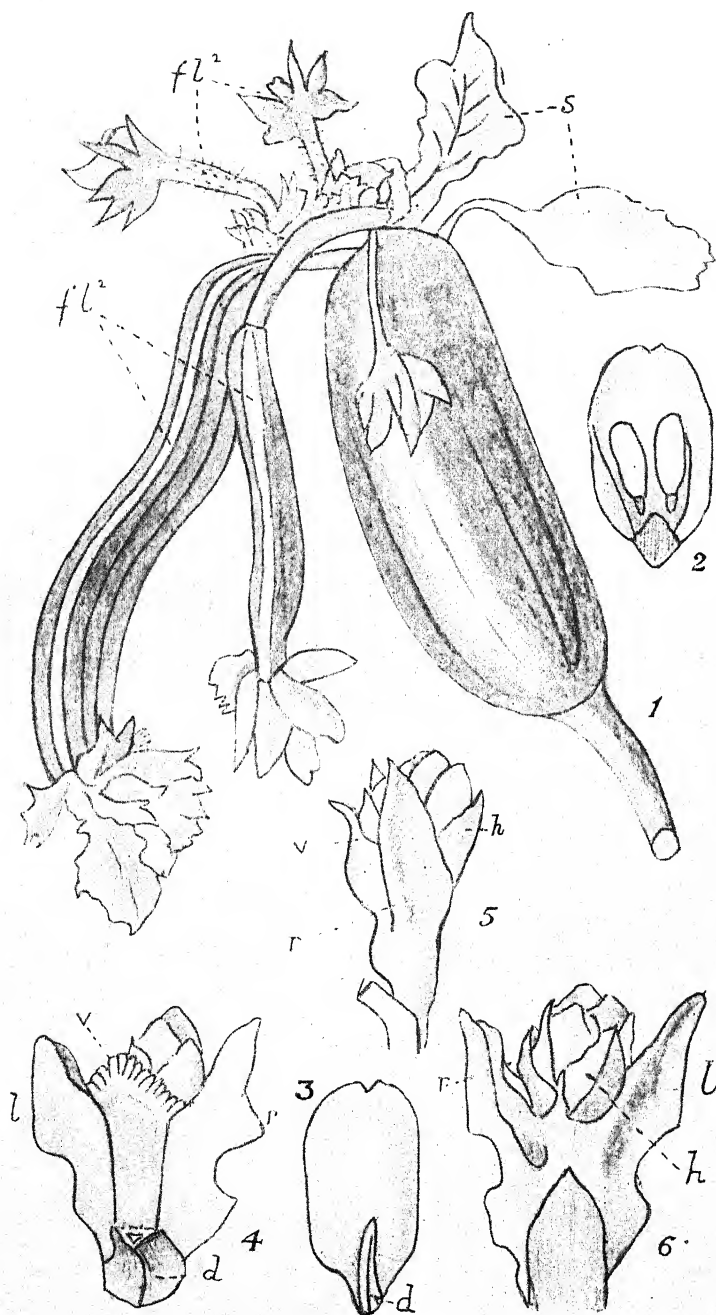
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PLATE XXXI.

FIGS.

1. *Cucumis sativus* (Cucumber). Secondary flowers axillary to the sepals (*s*) of the primary one. (G. S. Saunders.) p. 20.
- 2-6. *Picea excelsa* (Spruce). Fig. 2.—Normal ovuliferous scale (upper side). Fig. 3.—Lower side of same. Fig. 4.—Anterior view of abnormal ovuliferous scale and axillary bud. Fig. 5.—Lateral view of the same. Fig. 6.—Posterior view of the same. (*d*, bract; *lr*, two first leaves of bud (= divided ovuliferous scale); *v*, third constituent of scale; *h*, posterior member of second pair of bud-leaves.) (All after Willkomm.) p. 22.

PLATE XXXI



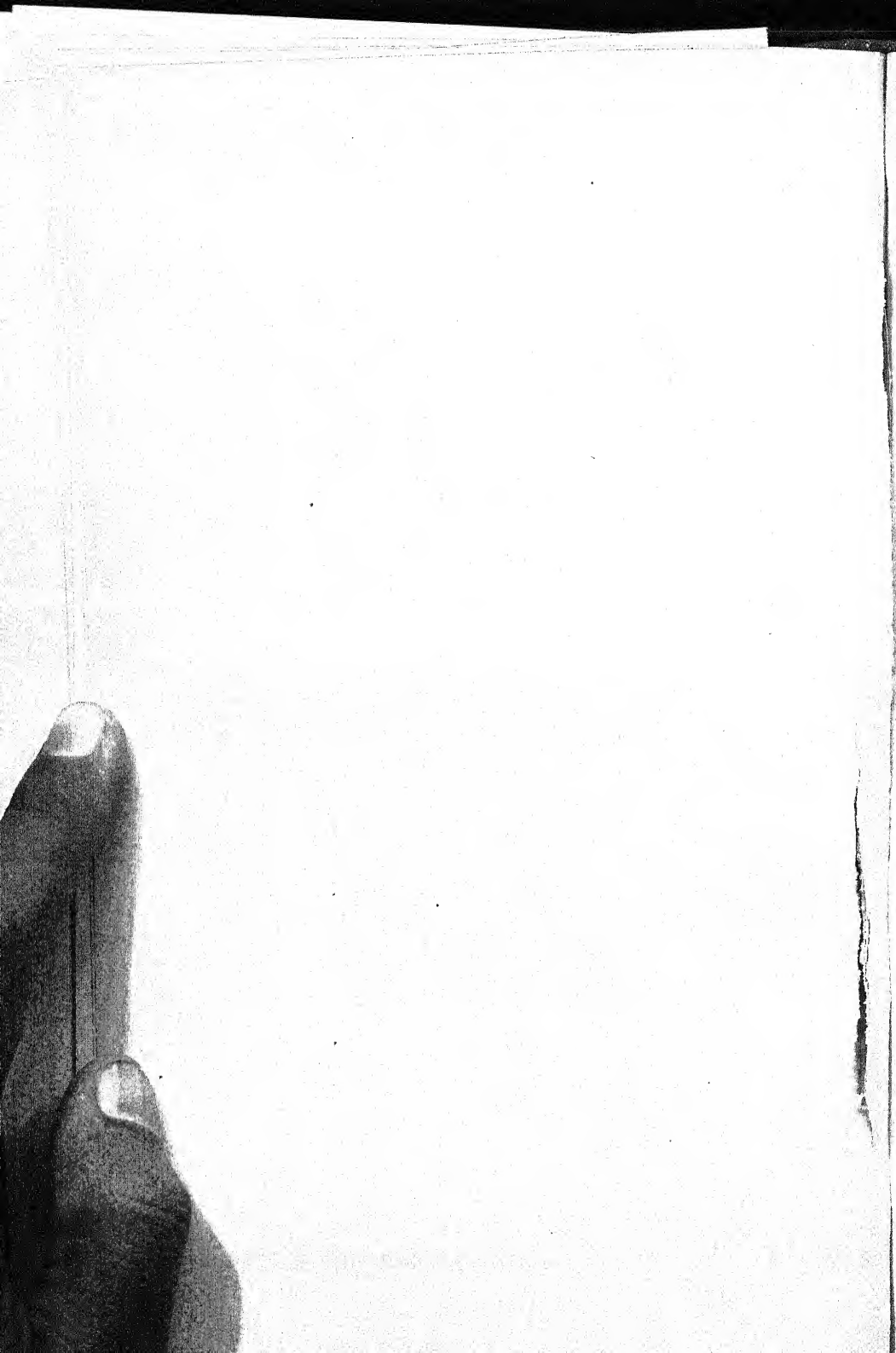
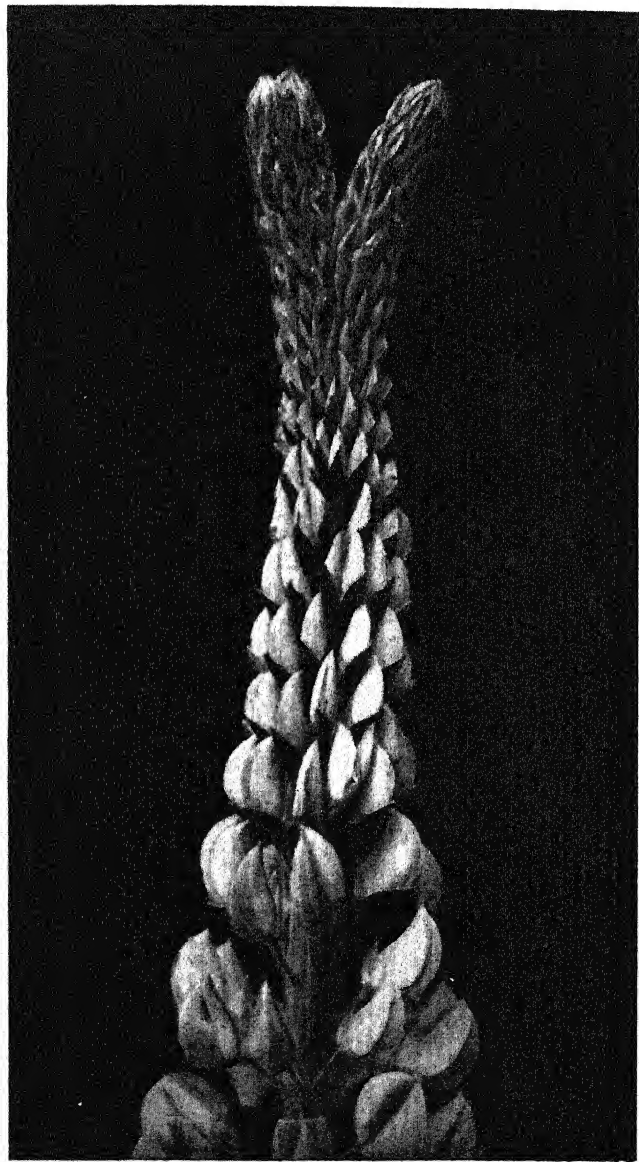


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PLATE XXXII.

Lupinus polyphyllus (Lupin). Bifurcating inflorescence.
p. 38.

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Plate 33

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PLATE XXXIII.

FIGS.

1. *Enanthe crocata* (Great Water-Dropwort). Fasciation of one of the primary rays of umbel. (G. E. Massee photo.) p. 39.
2. *Rosa damascena* (Garden Rose). Fasciation, showing ribbon-growth of peduncle and subdivision in one plane of primary flower to form great numbers of secondary flowers. p. 44.

PLATE XXXIII

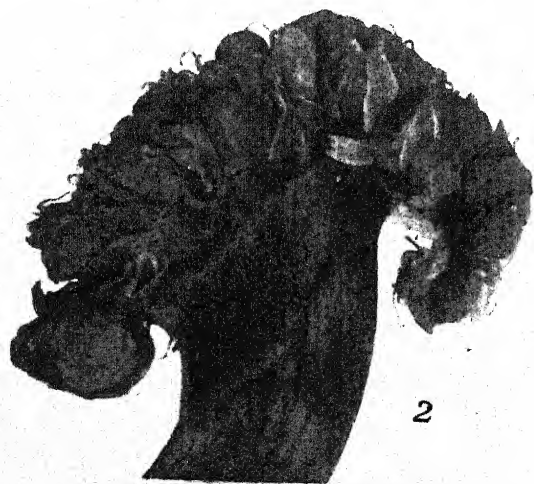
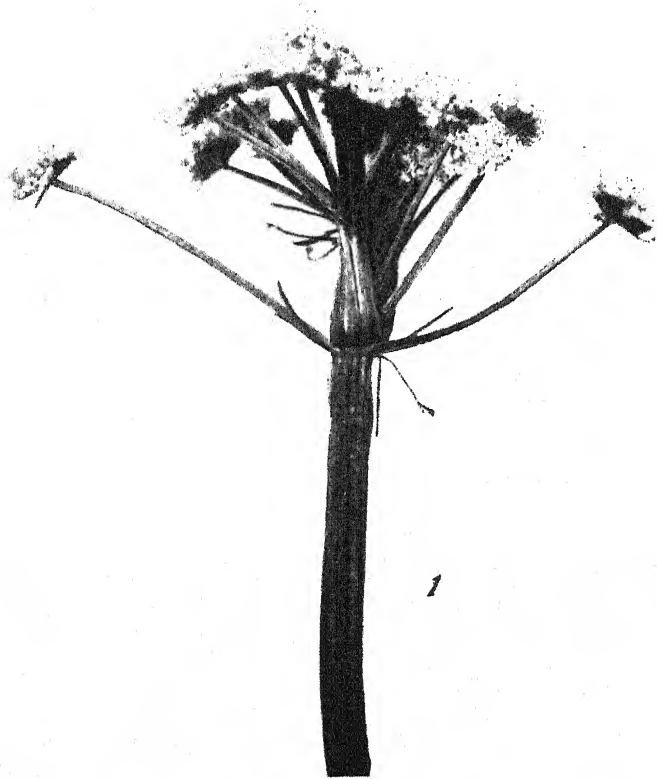


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PLATE XXXIV.

Digitalis purpurea (Foxglove). Fasciated terminal flower,
peloric in form. (G. E. Massee photo.) p. 49.

PLATE XXXIV



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PLATE XXXV.

Cypripedium insigne (Lady's Slipper). Posterior sepal divided into the original two sepals (s^2 , s^3). (G. S. Saunders and W. C. Worsdell.) p. 62.

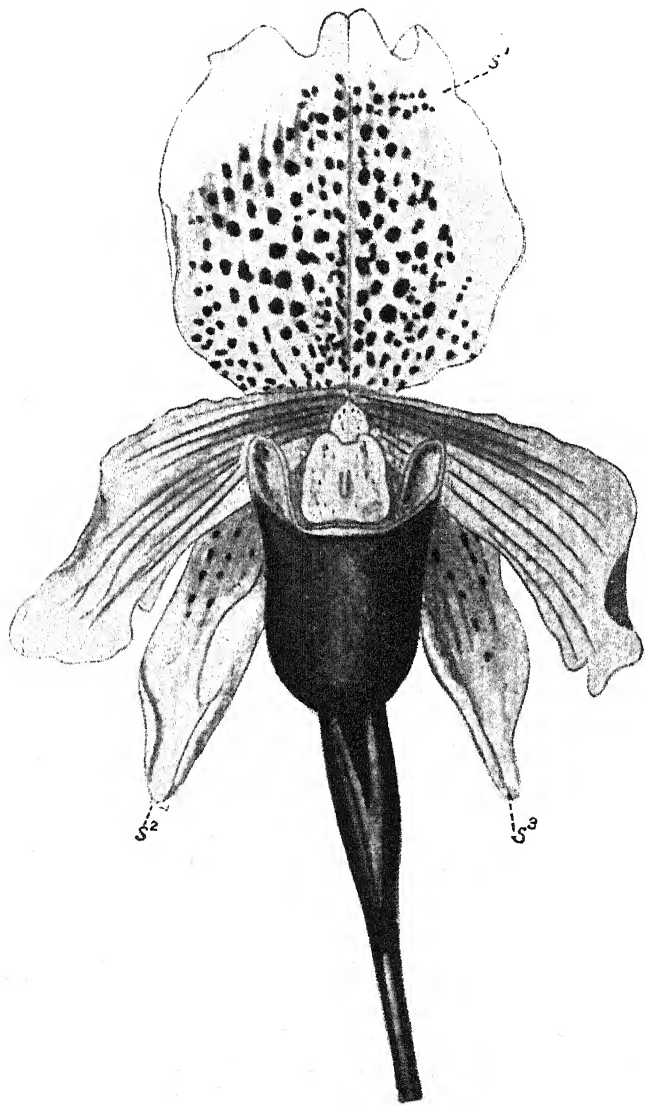


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PLATE XXXVI.

- FIGS.
1, 2. *Cypripedium Pitcherianum* (Lady's Slipper). Fig. 1.
—Flower with two labella (*lb*). Fig. 2.—Posterior
view of labella showing incomplete bipartition of
original single organ. (G. S. Saunders.) p. 66.

PLATE XXXVI

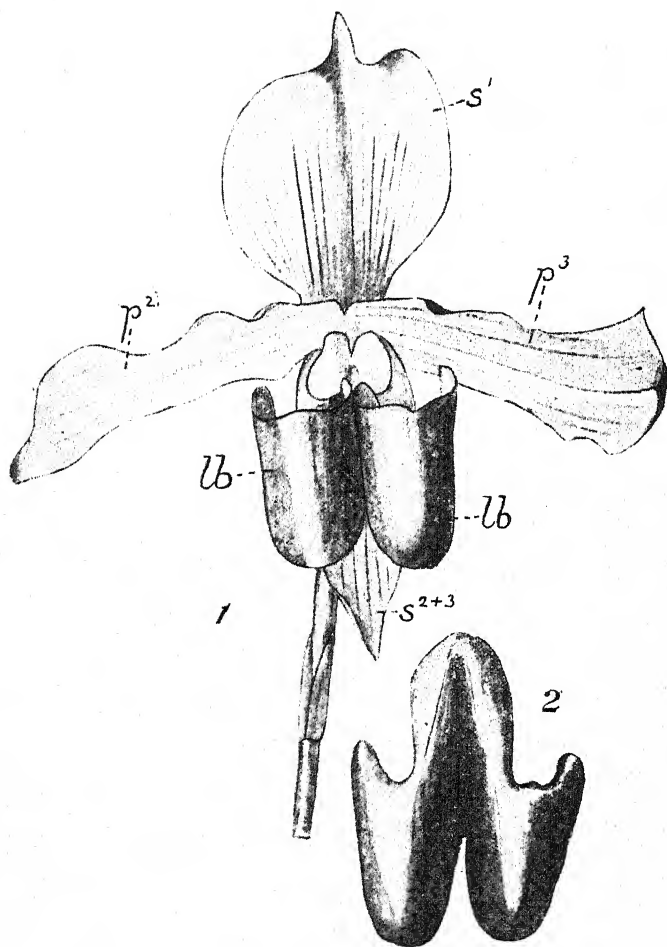


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PLATE XXXVII.

FIGS.

- 1, 2. *Euphorbia Cyparissias* (Cypress Spurge). Reappearance of sepals (*s*) below ovary. (After Schmitz.) p. 66.
3. *Petunia hybrida*. Serial dédoublement of stamrudiments (*st*) to form the double flower. Longitudinal section of half the flower-bud. (After Goebel.) p. 78.
4. *Butomus umbellatus* (Flowering Rush). Flower showing extra *epipetalous* whorl of three stamens, of which two have become united with stamens of the normal whorl. (After Celakovsky.) p. 80.
- 5, 6. *Odontoglossum grande* (an Orchid). Fig. 5.—Peloric flower with labellum in form of ordinary petal, and stamens A^2 and A^3 of the outer whorl present and fertile (pp. 82 and 94). Fig. 6.—Column of same flower showing three fertile anthers and three rostellæ. *s*¹, posterior sepal; *lb*, modified labellum. (After Schlechter and Fischer.) pp. 82 and 94.

PLATE XXXVII

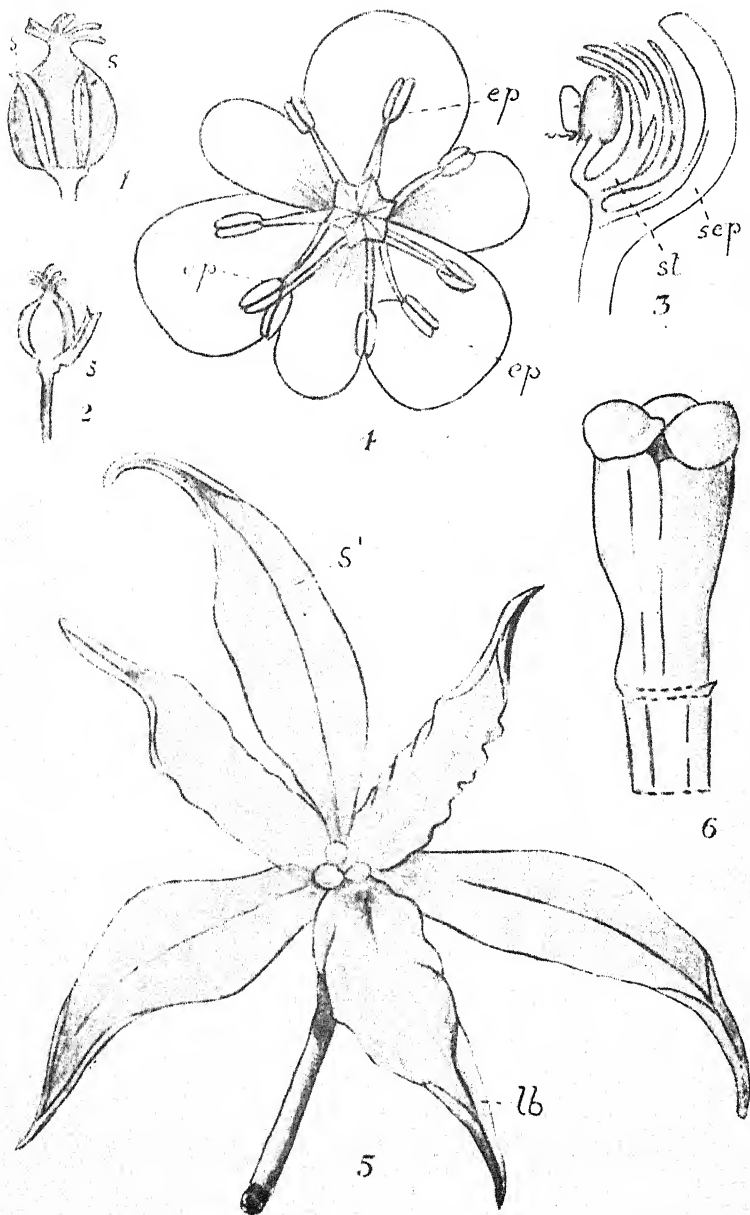


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PLATE XXXVIII.

FIGS.

1. *Prunus Cerasus* (Cherry). Double flower with two carpels partly foliaceous (in section). (After Turpin.) p. 93.
2. *Lycopodium rigidum* (species of Club-moss). Anterior view of sporophyll bearing two sporangia. (After Bower.) p. 102.
3. *Acer Pseudo-platanus* (Sycamore). Samara with two extra carpels. (G. S. Saunders.) p. 93.
4. *Vitis vinifera* (Grape-vine). Formation of a fruit in place of one of the adhering disks of tendril. (Original.) p. 95.
5. *Salix aurita* (Withe-tree). Hermaphrodite flower (original sex unknown). (After Velenovsky.) p. 96.
6. *Rosa indica* var. ("Green Rose"). Carpel bearing two marginal ovules. (After Masters.) p. 98.
7. *Ophioglossum palmatum* (species of Adder's-tongue Fern). Lower part of normal sporophyll showing numerous fertile "spikes" on upper surface. (After Bower.) p. 99.

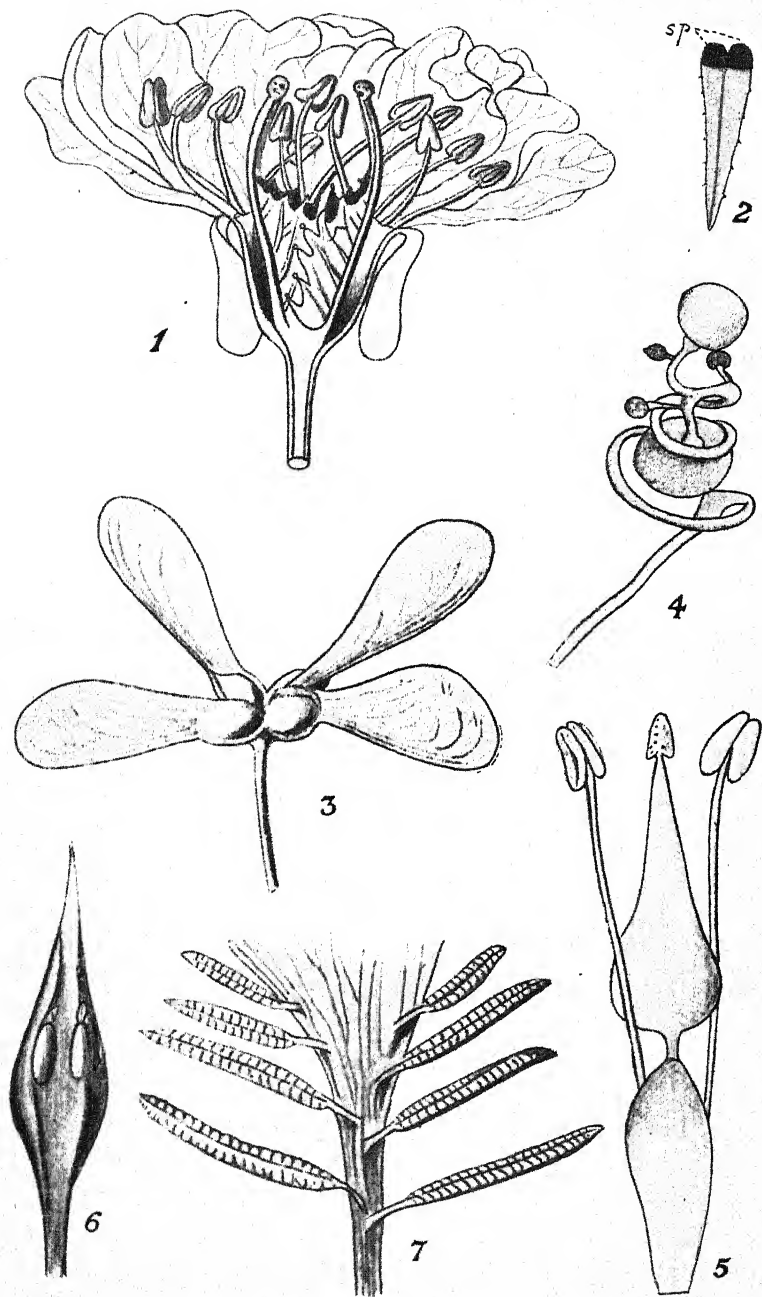


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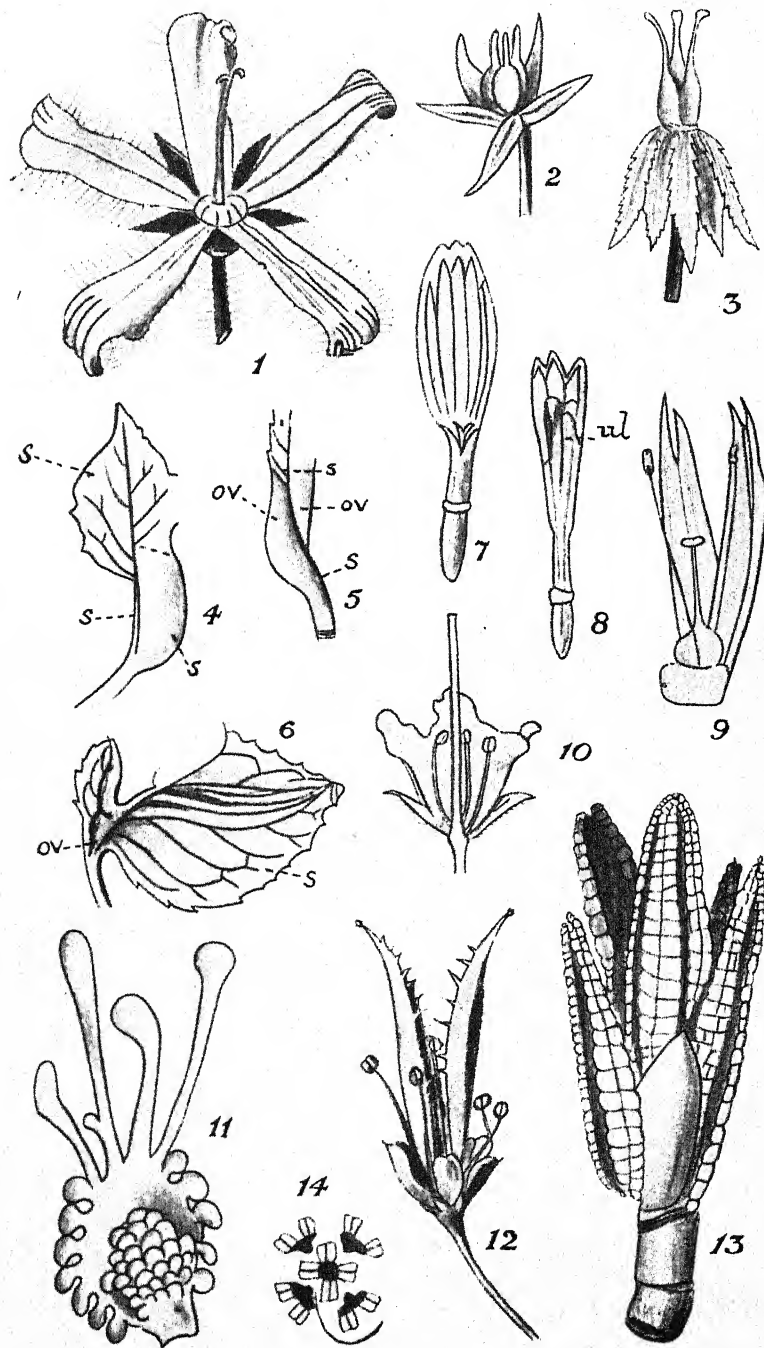
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PLATE XXXIX.

FIGS.

1. *Campanula Medium* (Canterbury Bell). Dialysis of calyx and corolla. (After De Candolle.) pp. 109 and 112.
2. *Enanthe crocata* (Great Water-Dropwort). Dissociation of calyx from carpels. (After Masters.) p. 109.
3. *Pyrus Malus* (Apple). Dissociation of calyx from carpels. (After Masters.) pp. 110 and 118.
- 4-6. *Fuchsia* sp. Figs. 4, 5.—Dissociation of a foliaceous sepal from ovary, with sepal-stalk decurrent along ovary wall; dotted line in fig. 4 shows upper limit of ovary. s, sepal; ov, ovary. (Original.) Fig. 6.—The same phenomenon. (After Masters.) p. 110.
- 7, 8. *Anthemis austriaca* (species of Chamomile). Fig. 7.—Normal ray-floret. Fig. 8.—Two-lipped ray-floret of var. *bilabiata*. ul, upper lip. (After Celakovsky.) p. 112.
9. *Primula vulgaris* (Primrose). Two free stamens inserted on the receptacle. (After T. G. Hill.) p. 115.
10. *Verbascum nigrum* (Dark Mullein). Three free stamens inserted on the receptacle. (After G. Henslow.) p. 116.
11. *Primula prænitens*. Pistil, showing dialysis of four styles and marginal ovules. (After Masters.) p. 117.
12. *Daucus Carota* (Carrot). The two carpels become dissociated from each other and from the calyx and at same time leafy and superior. (After Turpin.) p. 117.
- 13, 14. *Zea Maïs* (Maize, Indian Corn). Fig. 13.—Disruption of cob into its primitive branches. Fig. 14.—Ground-plan of same. (After Ascherson.) p. 58.

PLATE XXXIX



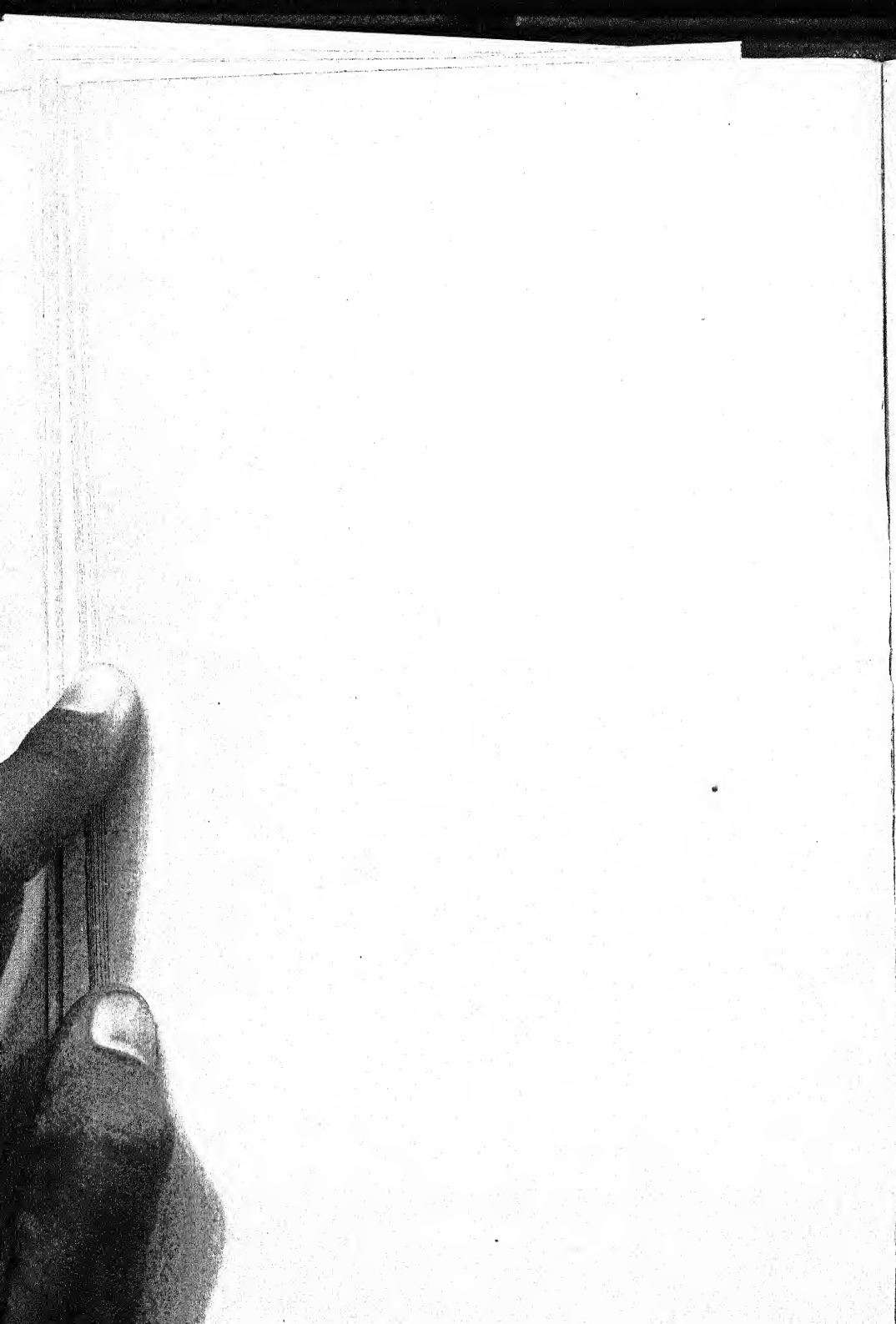


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PLATE XL.

FIGS.

1. *Saxifraga Cotyledon* (Pyramidal Saxifrage). Flowers transformed into a rosette of foliage-leaves. (G. S. Saunders and W. C. Worsdell.) p. 124.
- 2, 3. *Helenium autumnale* (Sneeze-wort). Fig. 2.—Proliferating ray-floret, showing virescent sepals; also dialysis of corolla and ovary. Fig. 3.—A ray-floret with virescent calyx. *sep.*, sepals; *pet.*, petals; *cp.*, carpels; *ax.*, proliferating axis; *cap*², secondary capitulum. (Original.) p. 127.
4. *Primula vulgaris* (Primrose). Flower with virescent petals. (G. S. Saunders and W. C. Worsdell.) p. 137.
5. *Cypripedium insigne* (Lady's Slipper). The two lateral petals changed into "lips" (labella). (G. S. Saunders and W. C. Worsdell) pp. 143 and 144.

PLATE XL

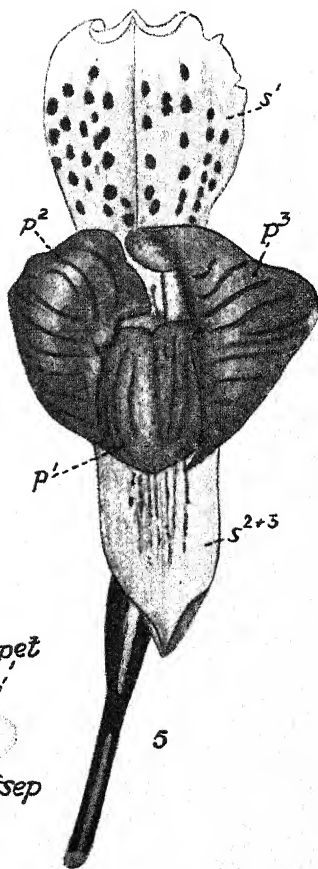
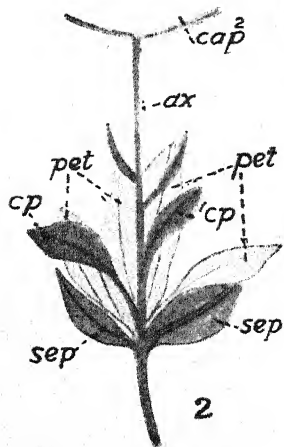
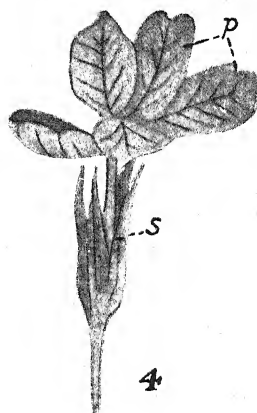
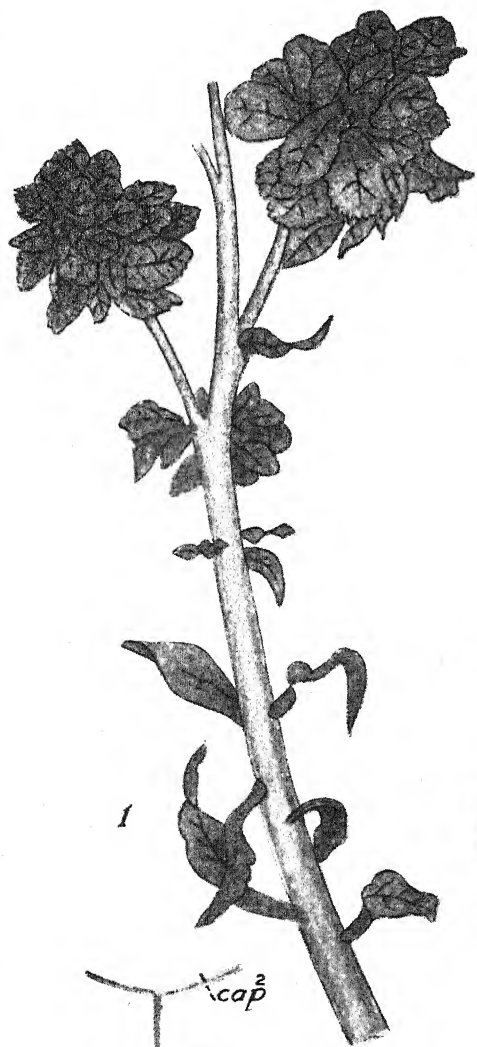


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PLATE XLI.

FIGS.

1. *Dianthus Caryophyllus* (Carnation). All floral members changed into sepals, spirally arranged and greatly increased in number. (Mingay photo.) p. 125.
- 2, 3. *Juncus lamprocarpus* (Closs, Strit). Fig. 2.—Normal inflorescence. Fig. 3.—Inflorescence transformed into a rosette of bracts. (J. Hutchinson photo.) p. 124.
4. *Barbarea stricta* (Yellow Rocket). Two flowers of inflorescence transformed into leafy shoots. (J. Hutchinson photo.) p. 124.
- 5-7. *Saxifraga ligulata* (Great Strap-leaved Saxifrage). Peculiar conformation of foliage-leaves, illustrating anther-structure. p. 162.

PLATE XLI



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PLATE XLII.

Figs.

1. *Rubus fruticosus* (Blackberry, laciniate var.). Calyx become leafy. (G. S. Saunders.) p. 126.
2. *Platanthera chlorantha* (Butterfly Orchis). The two lateral sepals are spurred. (After Hemsley.) p. 134.
3. *Fuchsia* sp. Flower with zygomorphic calyx. *s*, sepals; *p*, petals. (After Hildebrand.) p. 135.
4. *Viola collina*. Peloric flower caused by absence of spur from anterior petal (dorsal view). (After Velenovsky.) p. 148.
5. *Prunella vulgaris* (Self-heal). Peloric terminal flower. (After Peyritsch.) p. 149.
- 6, 7. *Ranunculus Ficaria* (Lesser Celandine). Fig. 6.— Flower seen from above, showing transformation of petals 4 and 5 into sepals IV and V. Fig. 7.— Calyx of same flower seen from below, showing the five sepals. (After Celakovsky.) p. 141.

PLATE XLII

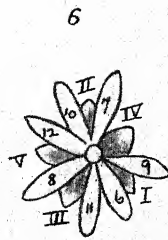
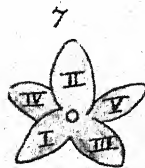
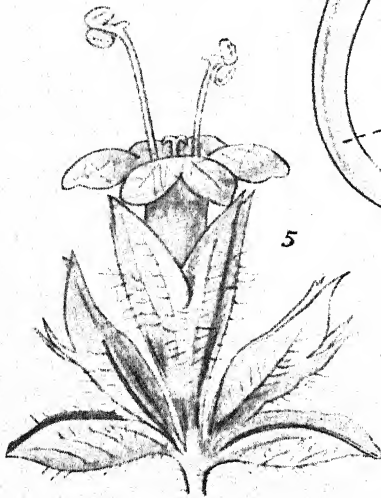
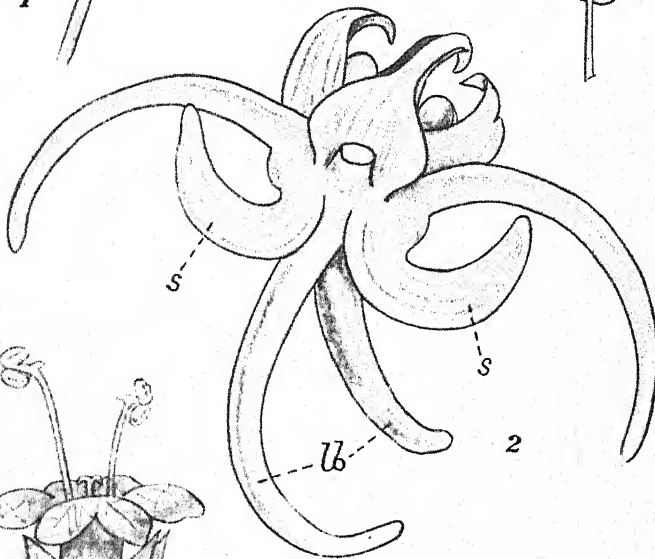
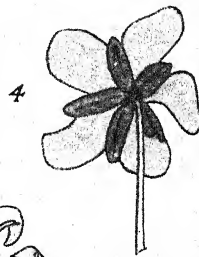
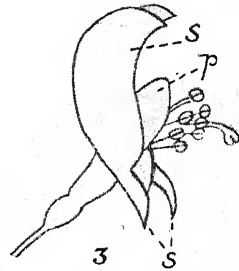
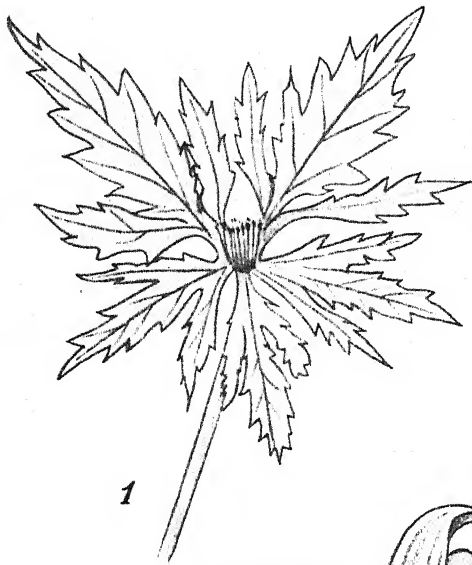


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PLATE XLIII.

FIGS.

- 1, 2. *Capsella Bursa-pastoris* (Shepherd's Purse). Flowers in which the corolla is replaced by four stamens (*st*). *sep*, sepals. In fig. 2 the calyx is removed. (After A. de Candolle.) p. 153.
- 3, 4. *Digitalis purpurea* (Foxglove). Flowers in which the corolla is replaced by five stamens. *ul*, *ll*, stamens replacing upper and lower lip respectively; *sep*, sepals. (After Miss E. Saunders.) p. 154.
- 5, 6. *Rosa indica* (Monthly Rose). Leafy stamens: transitions between foliage-leaves and stamens. (After Celakovsky.) p. 161.
7. *Dictamnus Fraxinella* var. *albus* (Burning Bush). Virescent anther. (After Celakovsky.) p. 162.
- 8-10. *Phlox paniculata* (Tall Garden Phlox). Foliage-leaf conformations illustrating anther-structure. Fig. 8.—Base of leaf. Figs. 9, 10.—Entire leaves. *us*, upper surface. (Original.) p. 162.
- 11, 12. *Hieracium glanduloso-dentatum*. Foliage-leaf conformations illustrating anther-structure. (After Celakovsky.) p. 162.
13. *Saxifraga ligulata* (Great Strap-leaved Saxifrage). Foliage-leaf with infolded apex, and a small ascidium on the lower surface. *us*, upper surface; *ls*, lower surface. (Original.) p. 164.
14. *Vitis vinifera* (Grape-vine). Two leaves united by the upper surfaces of their petioles (as far as dotted line). (Original.) p. 166.

PLATE XLIII

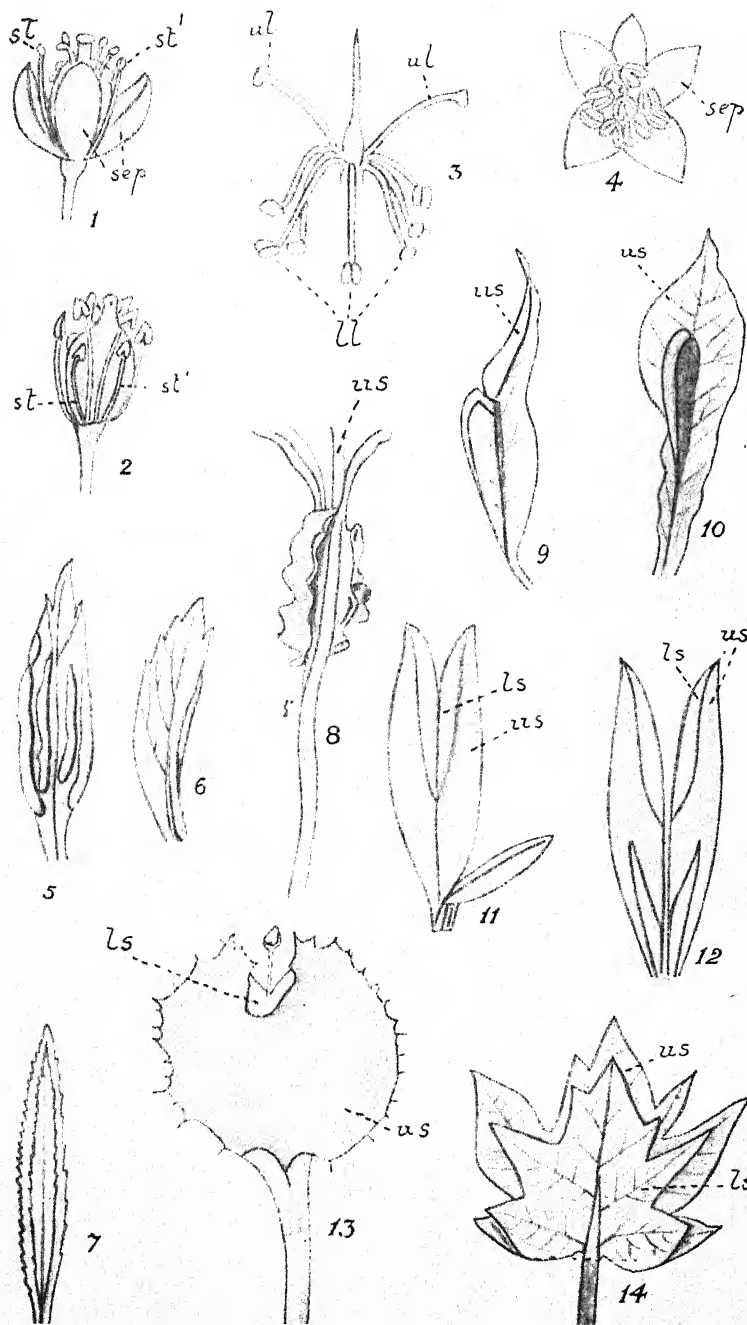




Plate 44

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PLATE XLIV.

FIGS.

1. *Caltha sagittata* (species of Marsh Marigold). Normal foliage-leaf; basal lobes not adnate to main part of blade. (Original.) p. 165.
2. *C. appendiculata* (species of Marsh Marigold). Normal foliage-leaf; up to dotted line the two basal lobes are adnate to midrib of leaf. (Original.) p. 165.
- 3, 4. *Jatropha Pohlana*. Leafy anther = two leaves united by upper surfaces. (After Müller (Argov).) Fig. 4.—Leafy anther, showing dichotomy, as in the *Hieracium* - leaf (Plate XLIII). (After Müller (Argov).) pp. 166 and 169.
5. Imaginary leaf to show fusion of two leaves by their dorsal surfaces. p. 169.
- 6-9. *Narcissus Tazetta* (Polyanthus Narcissus). Petaloid stamens. Fig. 6.—In form of ascidium. Fig. 7.—Infolded corona. Fig. 8.—Basal corona-lobes continuous by their inner margins with ventral lamellæ of anther. Fig. 9.—Shows corona-texture of lower part of ventral lamellæ. More deeply shaded parts have corona-texture and -colour. (After Celakovsky.) p. 179.
10. *N. Pseudo-narcissus* (Double Daffodil). Petaloid stamen with corona as two lateral lobes. (After Celakovsky.) p. 179.

PLATE XLIV

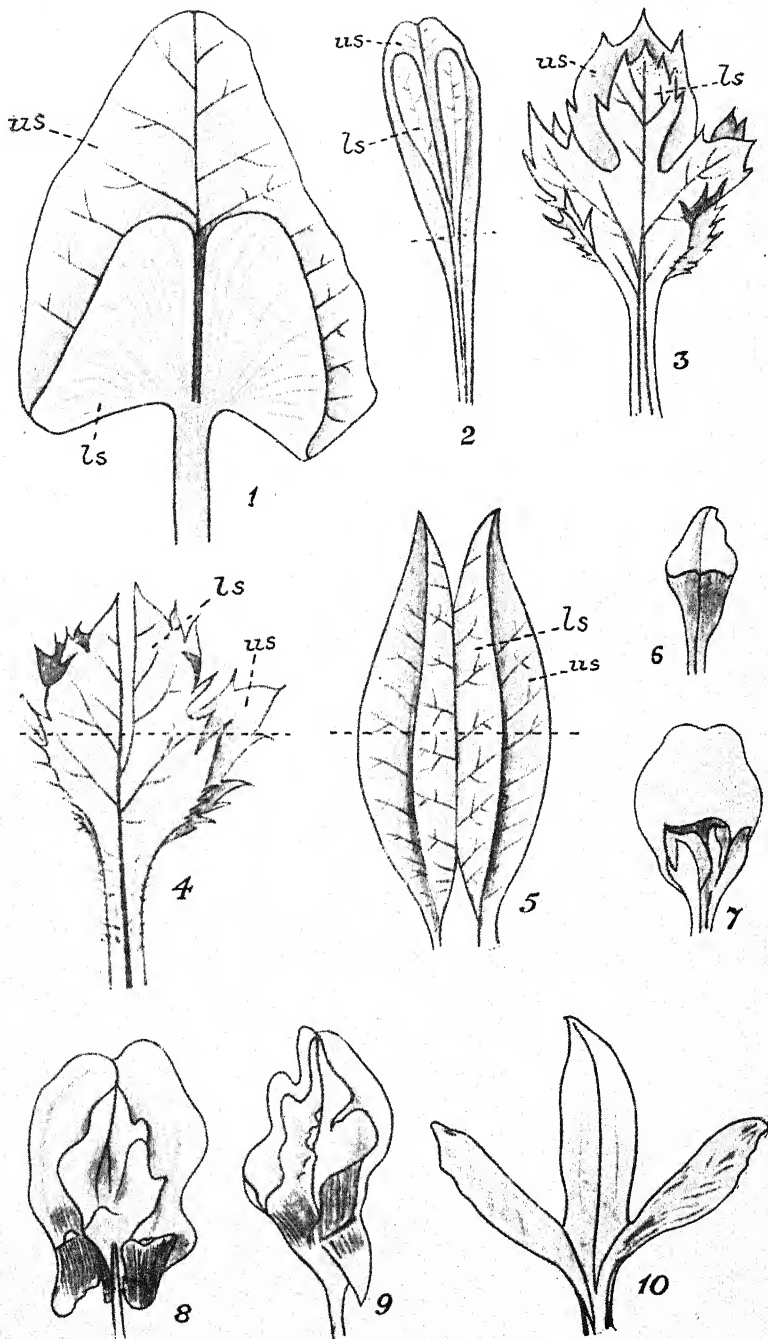


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PLATE XLV.

Papaver Rhœas var. (French Poppy). Transformation of
innermost stamens into carpels. p. 183.

PLATE XLV

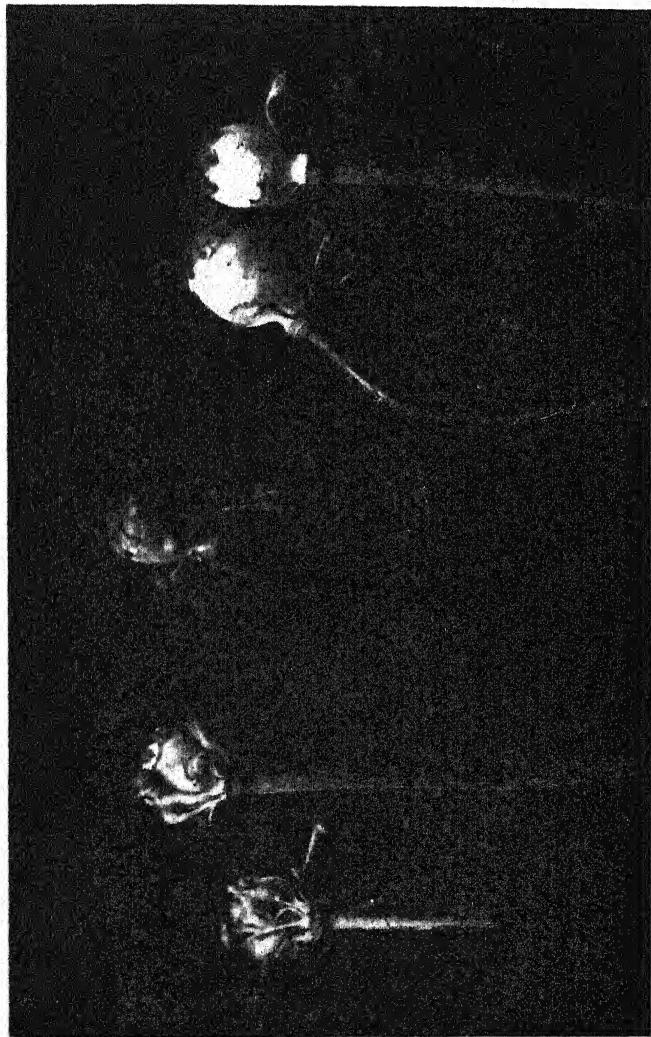




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PLATE XLVI.

FIGS.

- 1, 2. *Saxifraga ligulata* (Great Strap-leaved Saxifrage). Fig. 1.—Foliage-leaf illustrating anther-structure (slightly schematized). Fig. 2.—Foliage-leaf in form of ascidium. (Original.) pp. 162, 165, and 180.
- 3, 4. *Narcissus Tazetta* (*Polyanthus Narcissus*). Fig. 3.—Petaloid stamen in form of ascidium. Fig. 4.—Ditto, with distinct corona-lobe. *co*, corona. (After Celakovsky.) pp. 178–180.
- 5–7. *Primula vulgaris* (Primrose). Fig. 5.—Pinnate stamen bearing ovules; lowest pinna in form of a completely-organized carpel bearing a stigma; ventral placenta also present. Fig. 6.—A stamen bearing a median ventral placenta. Fig. 7.—A stamen whose ventral placenta is free except at extreme base. (After Masters.) p. 185.
8. *Euphorbia Cyparissias* (Cypress Spurge). Flower in which some stamens have become changed into carpels (*c*). (After Schmitz.) p. 190.
- 9–10. *Salix cinerea* (Grey Sallow). Fig. 9.—Transitional structures between stamens and carpels (from a male plant). Fig. 10.—Male flower whose stamens are changed into carpels. (Original.) p. 190.
11. *S. alba* var. *vitellina* (Golden Osier). Male flower whose stamens are in different degrees changed into carpels. *b*, bract; *an*, anther; *ps*, pollen-sacs; *cp*, carpel; *st*, stigma. (Original.) p. 191.

PLATE XLVI

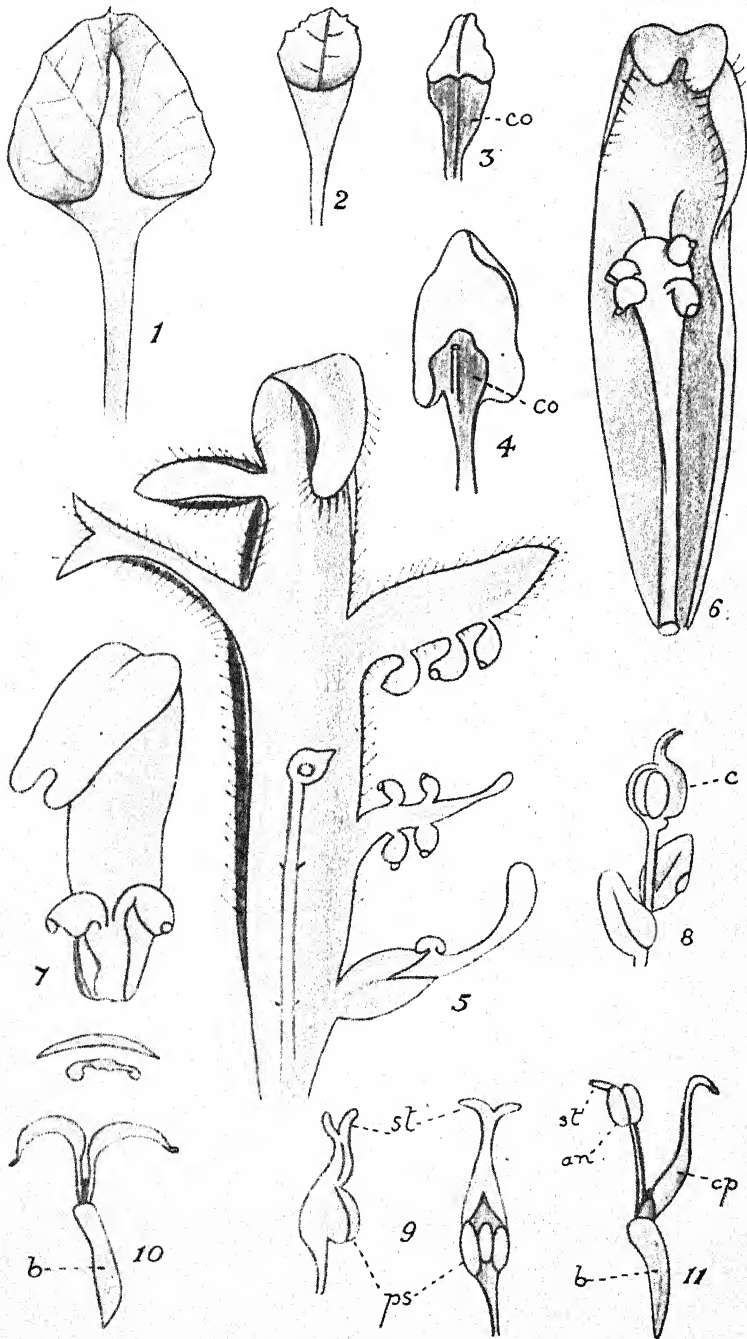


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PLATE XLVII.

FIGS.

- 1-5. *Primula vulgaris* var. (Polyanthus). The calyx of all flowers has become leafy. (J. Hutchinson photo.)
p 126.
- 6-9. *Zea Mâis* (Maize, Indian Corn). Different stages in the transformation of male panicles into female "cobs." (After Blaringhem.) p. 191.

PLATE XLVII



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PLATE XLVIII.

Figs.

1. *Tulipa Gesneriana* (Garden Tulip). Transverse section of anther bearing pollen-sacs and ovules. (Original.) p. 192.
2. *Rosa arvensis* (Field Rose). A stamen bearing polleniferous ovules (*ov*) and a stigma (*st*), *an*, anthers. (After Masters.) p. 193.
3. *Daucus Carota* (Carrot). Slightly virescent carpel bearing marginal ovules. (After Cramer.) p. 195.
- 4, 5. *Trifolium repens* (Dutch Clover). Virescent flowers. Fig. 4.—With a trifoliolate leafy carpel. Fig. 5.—With a unifoliolate leafy carpel. *cp*, carpel; *stp*, stipule; *co*, corolla; *cal*, calyx. (Original.) p. 194.
- 6-9. *Sisymbrium Alliaria* (Garlic Mustard). Figs. 6, 7.—Ovular leaflets. Fig. 8.—Diagram showing the three sets of laminæ. Fig. 9.—Diagram showing mode of enwrapping of nucellus by integuments. *f*, funicle; *oi*, outer integument; *ii*, inner integument; *n*, nucellus. (After Celakovsky.) pp. 196 and 197.
- 10, 12. *Trifolium repens* (Dutch Clover). Various forms of ovular leaflet. (After Celakovsky.) p. 197.
11. *Hymenophyllum* sp. (Filmy Fern). Pinnule, showing analogous structure to that of *Trifolium*. (After Celakovsky.) pp. 201-202.
- 13, 14. *Hesperis matronalis* (Dame's Violet). Ovular leaflets bearing more than one inner integument on the lower side. (After Celakovsky.) pp. 197 and 198.
15. *Cystopteris* sp. (Bladder Fern). Pinnule showing analogous position of indusium. (After Celakovsky.) p. 202.

PLATE XLVIII

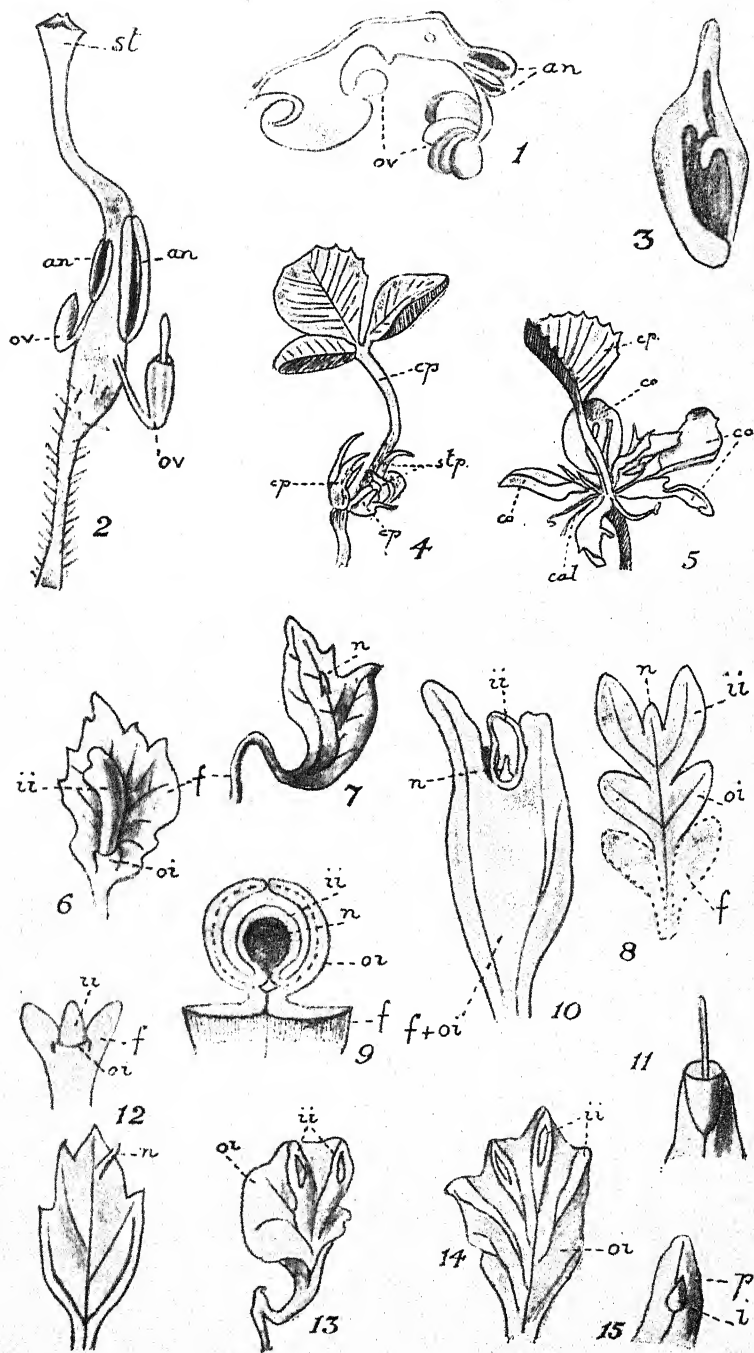


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PLATE XLIX.

FIGS.

1. *Aquilegia* sp. (Columbine). Partially virescent follicles bearing leafy ovules on their margins. (After Turpin.) p. 202.
2. *Trifolium repens* (Dutch Clover). Flower bearing a virescent carpel bearing leafy ovules on its margins. (After Turpin.) p. 202.
3. *Cyathea* sp. (Tree Fern). Pinnule bearing indusium and receptacle on lower surface. (After Celakovsky.) p. 202.
4. *Reseda lutea* (Wild Mignonette). Ovular leaflet. (After Celakovsky.) p. 202.
5. *Tulipa sylvestris* (Wild Tulip). Perianth-leaf. (After Celakovsky.) p. 202.
6. *Syringa vulgaris* (Lilac). Foliage-leaf. (After Celakovsky.) p. 200.
7. *Camellia japonica*. Virescent stamen. *fil*, filament. (Celakovsky.) p. 200.
8. *Backea diosmæfolia*. Ovary producing stamens in place of ovules. (After Masters.) p. 207.
9. *Begonia* sp. A carpel bearing an anther. *st*, stigma; *an*, anther. (Original.) p. 208.
- 10-13. *Equisetum maximum* (Horse-tail). Leafy sporophylls. Fig. 10.—Dorsal side of a sporophyll. Fig. 11.—Ventral side of same. Fig. 12.—Lateral view of a sporophyll. Fig. 13.—Dorsal view of same. (Original.) p. 211.

PLATE XLIX

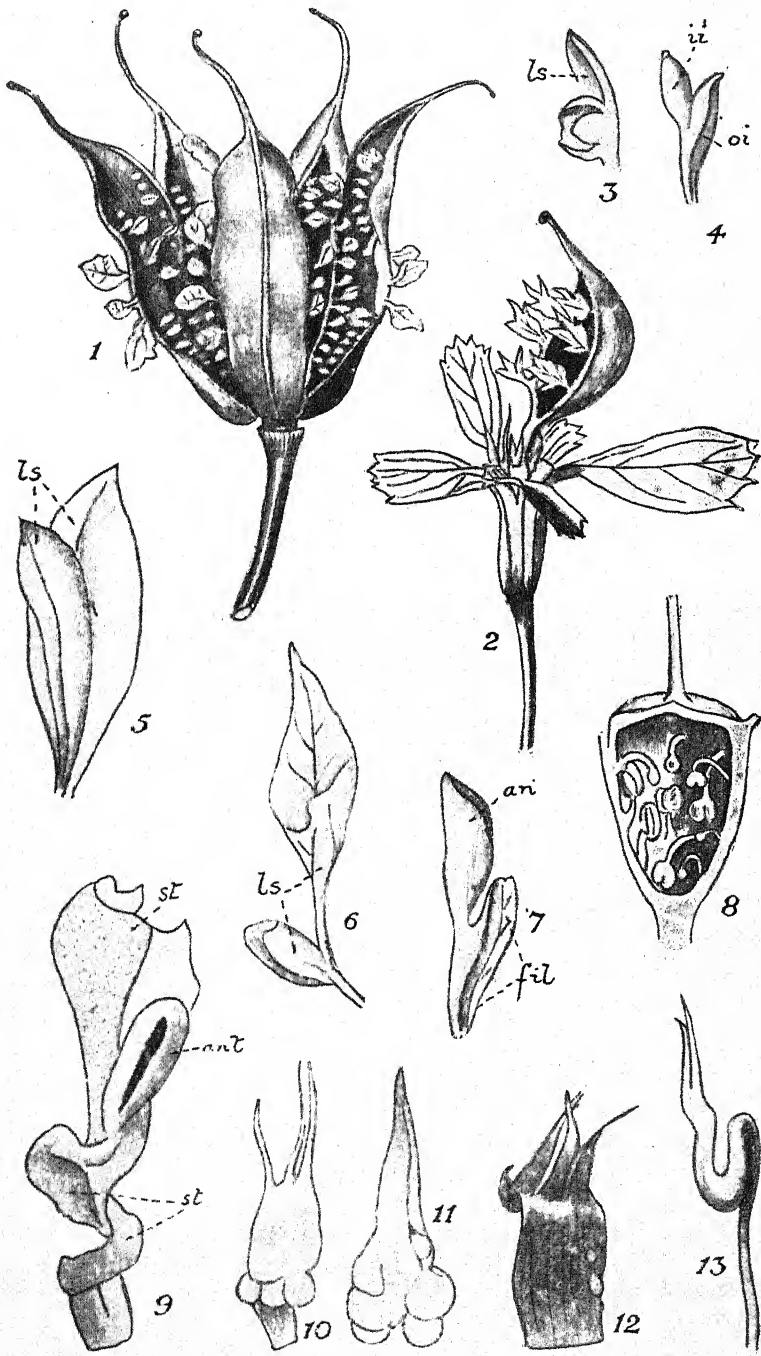


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PLATE L.

FIGS.

1. *Cypripedium superbiens* (Lady's Slipper). Adhesion of the two lateral petals to the posterior sepal, and suppression of the labellum. (G. S. Saunders and W. C. Worsdell.) p. 234.
2. *C. barbatum* (Lady's Slipper). Adhesion of the two anterior sepals (arising by division of the single one) to the lateral petals. (G. S. Saunders and W. C. Worsdell.) pp. 234 and 235.
3. *Cattleya Loddigesii* (an Orchid). Dimerous flower; lateral petals absent; two "lips" (labella) present. (G. S. Saunders and W. C. Worsdell.) p. 246.

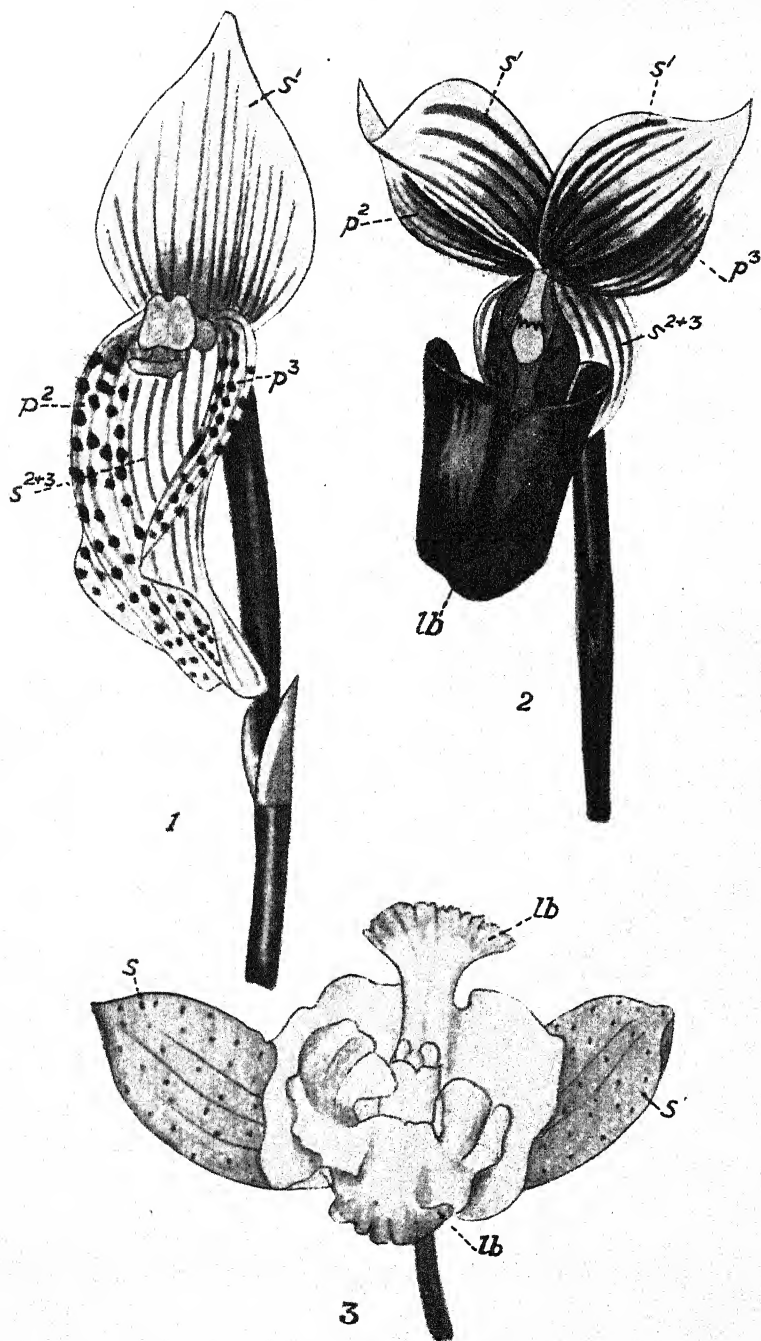


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PLATE LI.

FIGS.

1. *Amaranthus paniculatus*. Leaf bearing on its upper surface an inflorescence. (After Massolongo.) p. 233.
2. *Trichopilia tortilis* (an Orchid). Diagram of a dimerous flower showing adhesion of a sepal (*s*) to the column. (After Magnus.) p. 235.
3. *Prunus Cerasus* (Cherry). Section of a fruit in the condition of an "inferior" ovary. (After Carrière.) p. 235.
4. *Eucalyptus salicifolia* (species of Gum-tree). Flowers showing stages in synanthly. (After Migliorato.) p. 240.
5. *E. viminalis* (species of Gum-tree). Flowers showing stages in synanthly. (After Migliorato.) p. 240.
6. *Pedicularis sylvatica* (Red Rattle). Dual flower due to concrescence of two flowers. (After Wigand.) p. 239.
- 7, 8. *Lonicera Alberti* (species of Honeysuckle). Flowers showing stages in concrescence. Fig. 7.—Normal inflorescence of two flowers with fused ovaries. Fig. 8.—Abnormal inflorescence due to complete fusion of both flowers. (After Velenovsky.) p. 241.
9. *Trichopilia tortilis* (an Orchid). A flower whose perianth is reduced to a single posterior sepal (*s*) and a single anterior petal (*p*). (After Magnus.) p. 249.
10. *Papaver orientale* (Oriental Poppy). Flower with sympetalous corolla. (After Masters.) p. 250.
11. *Forsythia viridissima*. Flower with dimerous corolla (*p*). (After Velenovsky.) p. 251.

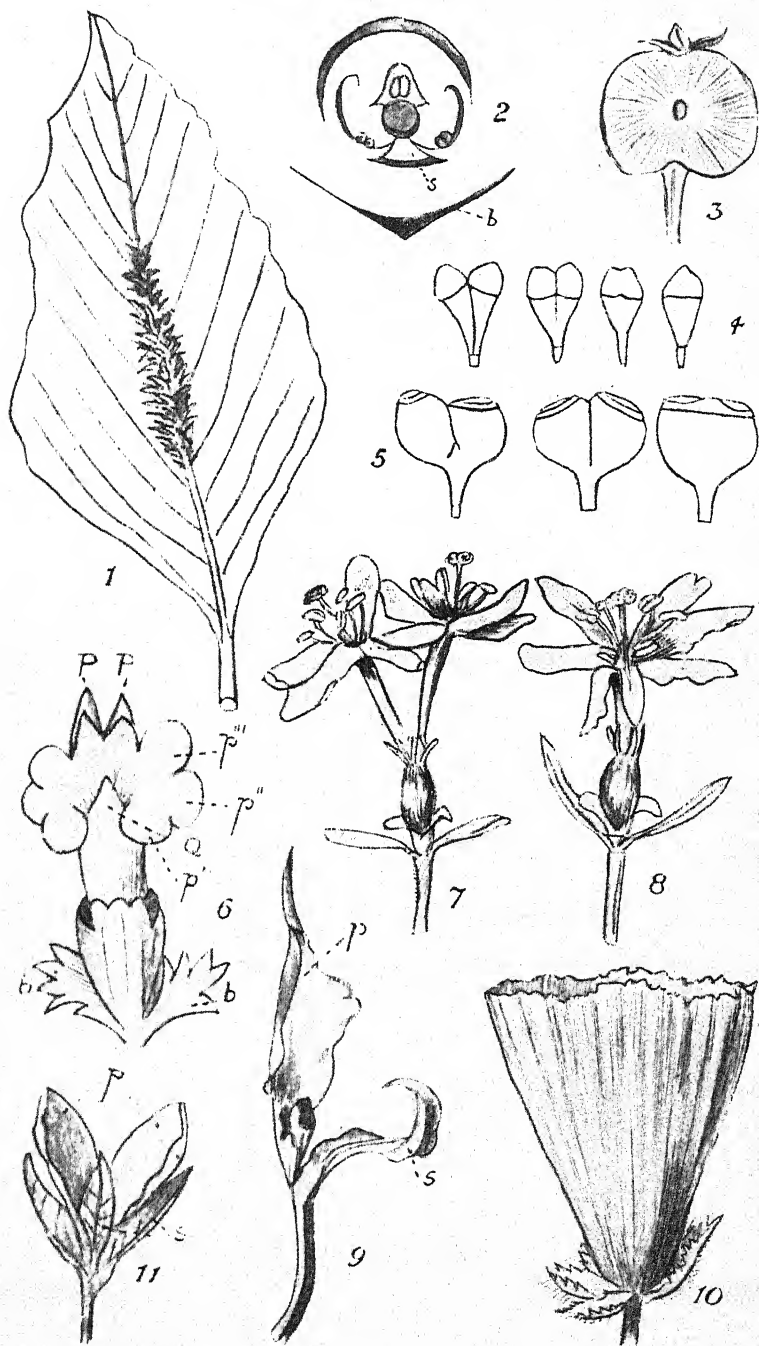




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PLATE LII.

Lilium candidum (Madonna Lily). A pentamerous terminal
flower. p. 242.

PLATE LII

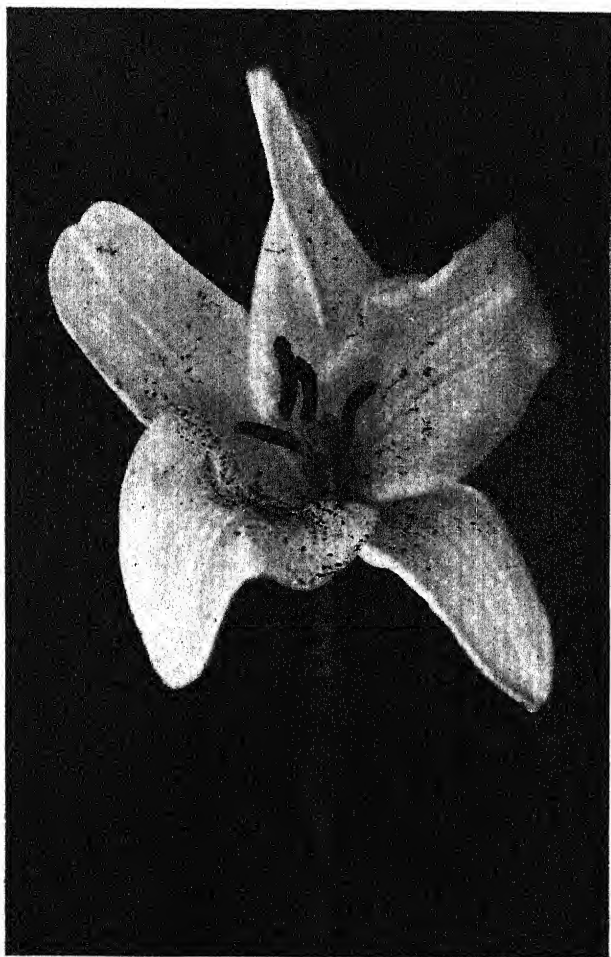


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PLATE LIII.

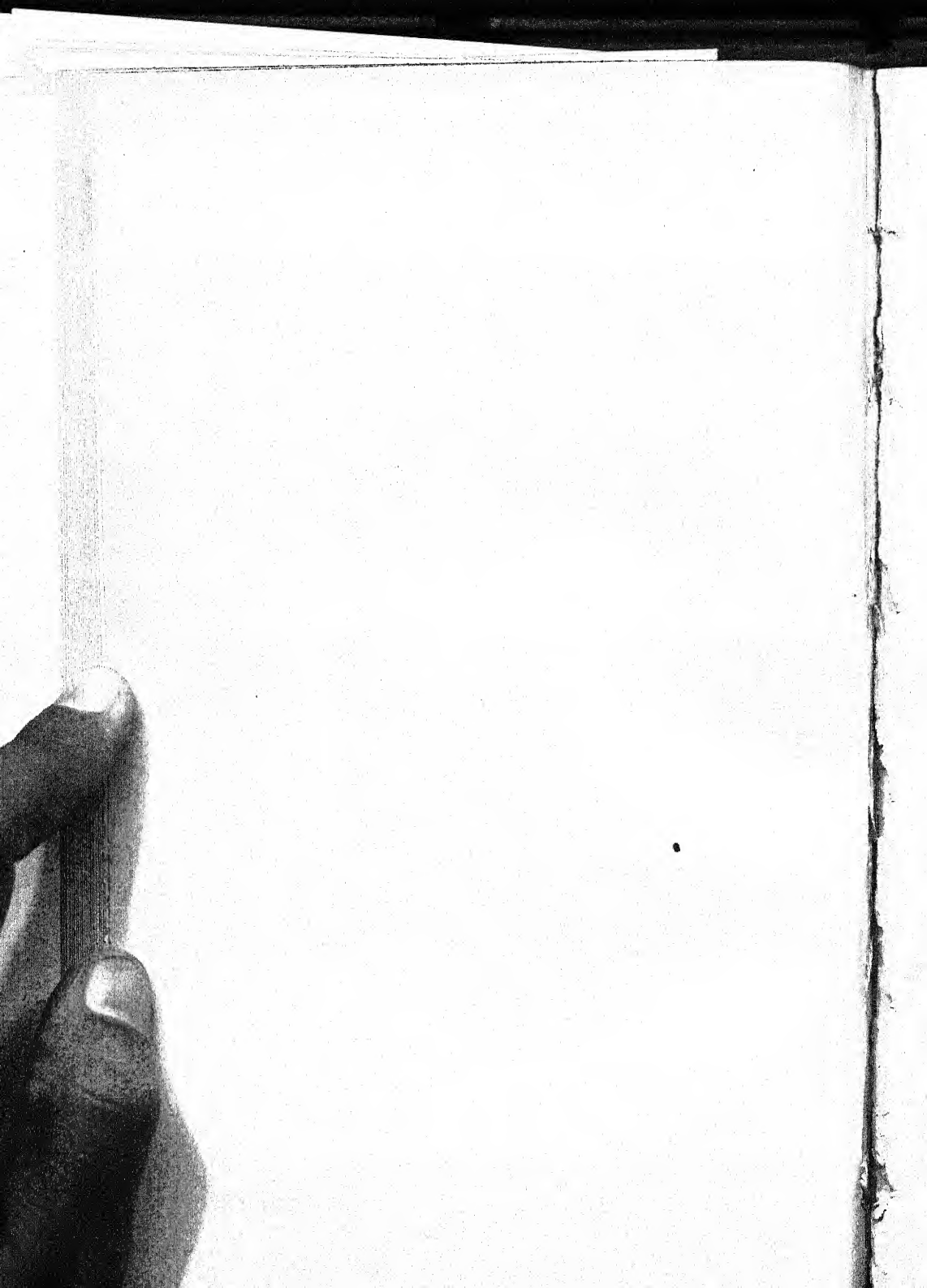
Dendrobium Wardianum (an Orchid). A flower showing the two lateral petals united to form a single posterior petal. (Mrs. M. E. L. Cox.) p. 250.

PLATE LIII



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